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SOME AMERICAN MEDULLOSAS[1]

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The continued discovery of new species of the polystelic stems referable to the genus *Medullosa* emphasizes the conspicuous role that these plants played in the Pennsylvanian floras of the United States. Almost every large collection of coal balls that is studied reveals a specimen or two that differs in some way from those previously described. Although it has been impossible to define species limits with definite clarity when the specimens are fragmentary, poorly preserved, or represent only a short segment of the stem, it seems more than likely that most recorded American species are valid.

Those of us who have worked with these plants assumed some time ago that as the sources of material were more extensively explored our efforts would tend toward working out fine details rather than reporting ever more bizarre forms. Actually the reverse has proved to be the case, and the occurrence in recent collections of specimens of greater stem length has permitted more satisfactory study of variable characters such as stelar number.

One of the most notable contributions to our knowledge of the Medullosas is the recent description of *M. heterostelica* by Stewart and Delevoryas (1952). Although it is a bi-stelar stem the two steles divide in the nodal region to form a complex of twenty or more, some of which contribute to the petiole traces, whereas others reunite, the stem becoming bi-stelar again above the node. Had this specimen been found in a more fragmentary condition, descriptions of several "species" might well have resulted. As it is, the evidence suggests that stelar number is a reliable taxonomic character provided that a representative specimen of the stem is available.

The present account deals with several *Medullosa* specimens that have come to light in the paleobotanical laboratory of Washington University since Baxter's contribution in 1949. Certain of these add to our knowledge of the distribution of previously described species; others are distinctly new and present what we

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believe to be highly significant information bearing on the problem of the taxonomic significance of stelar number.

MEDULLOSA THOMPSONII Andrews

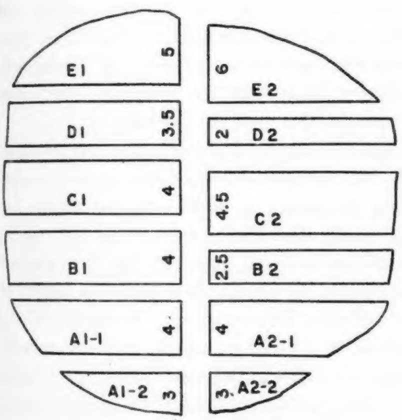
Two specimens referable to this species are present in our collections; both come from southeastern Kansas. One (No. 721) presents three steles (fig. 2), measuring 5 × 2.5 mm., 6 × 2.5 mm., and 2 mm. in diameter respectively and compares closely with the type specimen described from Iowa (Andrews, 1945). The second specimen is of interest because of its length and the type of stelar changes that occur. This stem, found in coal ball No. 713, is approximately 23 cm. long. No recognizable plant remains were evident on the exterior of the coal ball to guide the initial cut, and by chance the stem was dissected in a nearly median longitudinal plane. This seemed unfortunate at first, although it has materially aided us in following the changing stelar morphology through the length of the specimen. The plane of this initial cut accounts for the conspicuous break in certain of the cross-section illustrations (figs. 5-7).

Text-figures 1 and 2 show, respectively, a profile of the coal ball and a sketch of the stelar system indicating the divisions and fusions that take place. In the A1-2 and A2-2 blocks three steles (fig. 6) are present. These are enclosed by a clearly defined internal periderm that does not exceed 0.5 mm. in width and consists of rather thin-walled nearly cubical cells that present essentially the same appearance in transverse and radial sections. The steles at this point measure 13 × 9.5 mm., 11.5 × 6 mm., and 20 × 7 mm. In passing through the A1-1 and A2-1 blocks two of the steles fuse; the resultant two steles (fig. 7) measure 14 × 7.3 and 21.5 × 8 mm. Further divisions and fusions are indicated in text-fig. 2 as follows: In passing through the B blocks a stele divides, revealing three steles on the upper surface; in passing through the C blocks a fusion takes place, revealing two steles on the lower surface of D1 and D2; finally a small stele separates from one of the two steles, revealing three steles on the lower surface of the E blocks. Although the phloem is partly preserved, all stelar dimensions refer to the wood only.

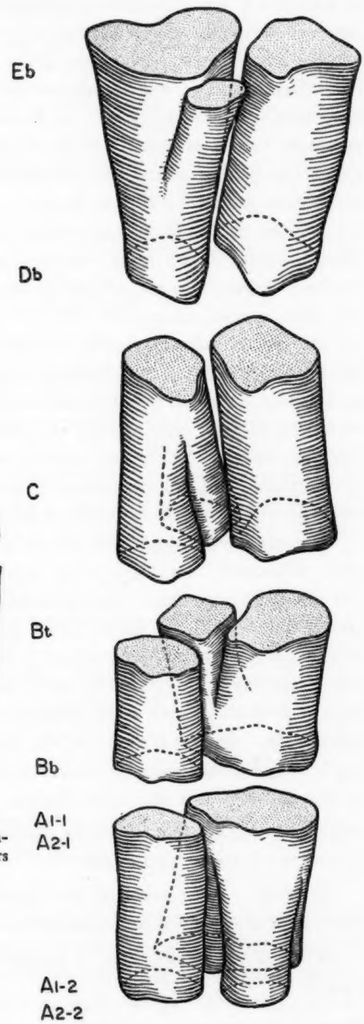
The secretory canals, which average about 0.3 mm. in diameter, are confined chiefly to the fiber zone of the cortex.

The primary body (fig. 3) contained a considerable amount of parenchyma, although this has decayed for the most part, leaving only the primary tracheids. The departing primary petiole strands are large and accompanied by little or no secondary wood. Through the length of this specimen there are at least two petioles that depart from the stem. It is especially important to note this, since obviously the type of nodal anatomy here is quite in contrast with that described for *Medullosa heterostelica*. This point will be considered in further detail under the description of the specimen that we are assigning to *M. heterostelica*.

The affinities of this stem seem to lie closest to *Medullosa distelica, M. anglica,* and *M. thompsonii,* but particularly the last. It differs from *M. distelica* in that



Text.-fig. 1. Profile of coal ball No. 713 containing specimen of *Medullosa thompsonii.* Numbers indicate thickness of blocks in centimeters.



Text-fig. 2. Restoration of the stelar system of *Medullosa thompsonii* (No. 713). Letters refer to the approximate position in the profile (text-fig. 1).

it presents a less constant association of secretory canals and fiber strands; an internal periderm which attains only about one-third to one-fifth the thickness of that of *distelica*; and in the stelar system the endocentric development of the secondary wood is not nearly so strongly pronounced nor as constant in our specimen. In comparing it with M. *anglica* it also appears to possess less abundant secretory canals associated with the fiber strands (Scott, 1899, pl. 12, fig. 14), somewhat smaller steles, and the secondary wood around the departing leaf traces is not retained in the Kansas fossil.

Almost every Medullosan stem discovered in American coal balls displays characteristics which tempt one to set up a new specific entity, or which at least render it difficult to assign the specimen with confidence to an established species. The four species assigned by Schopf (1939) to his subgenus *anglorota* as well as M. *thompsonii* (Andrews, 1945) and the species described more recently by Baxter (1949) are certainly all closely related. With some species the relationship is so close as to render very problematical the dividing line between species and varieties; we refer here to such specimens as M. *anglica* and its varietal forms (var. *thiesseni*, Schopf, 1939; var. *ioensis*, Andrews and Kernen, 1946), M. *thompsonii*, M. *elongata*, and M. *distelica*. Distinctive characters are somewhat more pronounced in certain others such as M. *endocentrica* and M. *primaeva*.

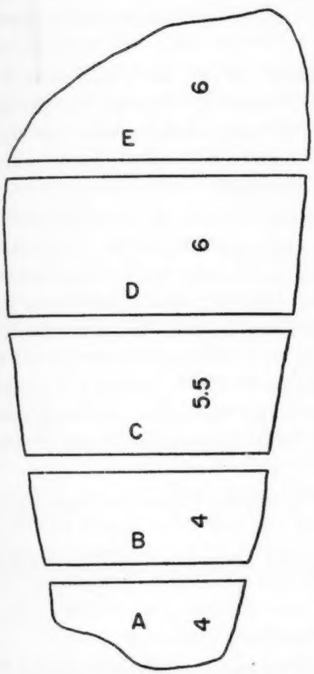
The taxonomic treatment of the specimen described above is admittedly somewhat arbitrary. Its affinity lies with the *anglica-distelica-thompsonii* complex, and the most expedient way of handling it appears to be to assign it to the last species mentioned. It differs from previously described specimens of this species only in its somewhat larger size. It is of real interest, however, for the information it conveys regarding the stelar anatomy. A seemingly significant length of stem is present to give some indication of what characters may be taxonomically dependable. Some variation in the centricity of the secondary xylem is evident, but it could at no point be closely compared with the extreme excentricity found in M. *distelica* and M. *endocentrica*. Within certain limits, which admittedly cannot be defined quantitatively, the degree and form of excentricity in *Medullosa* stems appear to be significant.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

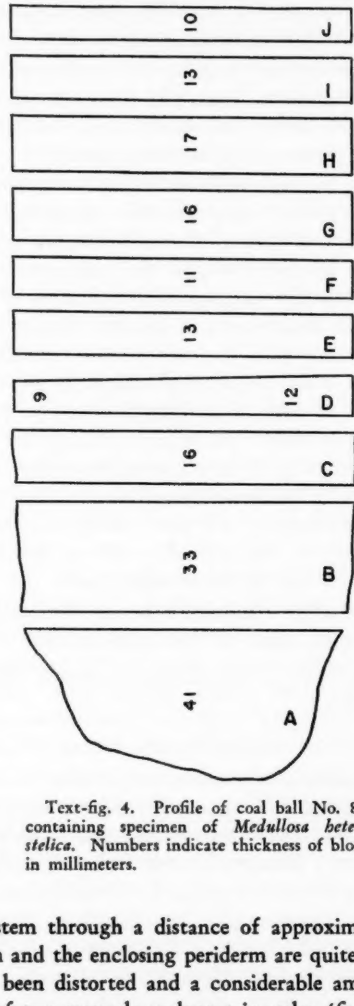
Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

MEDULLOSA DISTELICA Schopf

Another *Medullosa* specimen (No. 688) from the West Mineral, Kans., locality appears to be referable to this two-stelar species described by Schopf (1939) from the No. 6 coal of Illinois. It is basically a two-stelar specimen but presents certain variations which seem significant in furthering our knowledge of what may be considered to be specific boundaries in the genus.



Text-fig. 3. Profile of coal ball No. 688 containing specimen of *Medullosa distelica*. Numbers indicate thickness of the blocks in centimeters.



Text-fig. 4. Profile of coal ball No. 819 containing specimen of *Medullosa heterostelica*. Numbers indicate thickness of blocks in millimeters.

It has been possible to follow the stem through a distance of approximately 10 cm. (text-fig. 3). The stelar system and the enclosing periderm are quite well preserved, but the cortical tissues have been distorted and a considerable amount lost. In block *A* the stem is composed of two strongly endocentric steles (fig. 4). In the stem's course through the lower part of block *B* a small stele separates from one of the original two, producing a three-stelar system. After another 4 cm. the two-stelar phase is resumed, but since the preservation is poor beyond this point it has not been possible to determine whether any other changes take place.

The two principal steles measure about 18 × 6 mm. and 14 × 5 mm.; taking into account the obvious crushing, they measured approximately 18 × 8 mm. and

14 × 7 mm. in life. The small branch stele is nearly round in cross-section, measuring 5 mm. in diameter.

The primary body of each stele consists of scattered groups of tracheids and abundant parenchyma (fig. 9). A similar ratio occurs in *Medullosa endocentrica* (Baxter, 1949), presenting a rather striking contrast to certain other species such as *M. primaeva* and *M. thompsonii.*

In the type specimen of *M. distelica* (Schopf, 1939) the preservation of the primary wood was poor. The position of the protoxylem elements was not determined; and even in the well-preserved primary wood of the present specimen it is not possible to locate with certainty any regular position of protoxylem elements, so few and scattered are the primary tracheids.

The organization of secretory canals and fiber strands in the outer cortex or rind seems quite distinctive. An especially well-preserved portion of a petiole is shown in fig. 17, although essentially the same relationship may be observed in the stem. Starting at the outside it may be noted (fig. 10) that the secretory canals reach to within less than 1 mm. of the periphery. Here they are minute, the smallest being about 0.1 mm. in diameter, and are closely associated with the fiber strands. The canals increase in diameter toward the inside, reaching a maximum of approximately 2.5 mm. Within the rind proper the canals are conspicuously enclosed on three sides by a fibrous sheath. Only the outermost canals have an inconspicuous sheath or none at all.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

MEDULLOSA HETEROSTELICA Stewart & Delevoryas

Shortly after Stewart and Delevoryas (1952) described *M. heterostelica* from West Mineral, Kans., the present writers collected from the same locality a coal ball (No. 819) containing a stem which displays strikingly similar gross morphology. The stem has two steles which divide into more than fourteen, presumably in the nodal region. It differs from the type specimen, however, in two ways:

1. The two original steles in No. 819 measure about 16 mm. in diameter (xylem only) and are radially symmetrical with reference to both primary and secondary wood. The steles of the type specimen measure 5 × 8 mm., being less than one-half the diameter of those in our specimen.

2. The over-all size and form comparison is also reflected in the primary wood. The ratio of tracheids and parenchyma in the primary wood of the two seems to be comparable; but in No. 819 the size of the tracheids is conspicuously greater, and the primary body is nearly circular, whereas that of the type specimen is elongate.

A wholly satisfactory comparison of the two is impossible since the cortical tissues and leaf bases of our specimen are not preserved. It is, therefore, only on

the characters cited above that a decision as to specific identity can be made.

The chief point of interest that the specimen presents is the remarkable multiplication of steles in what we assume is the nodal region. This is in notable contrast to the stelar anatomy of any other species of *Medullosa,* and it is of course important to determine whether it is a specific character in itself. The evidence to date indicates that some species did not follow this pattern, whereas with others (based on short or fragmentary specimens) we cannot be certain.

A profile of the coal ball is shown in text-fig. 4. The stem appears about midway through block *A* and runs through the remainder of the specimen, totaling about 15 cm. As an introduction to a more detailed description it may be noted first that the stelar system consists of two steles, each of which gives off numerous branches which continue to divide and fuse. Although there is some interfusion between these two "systems," they tend to remain distinct. Beginning about midway through block *A* two steles make their appearance (fig. 11). They measure approximately 16 mm. in diameter, are essentially circular in cross-section, and have uniformly developed secondary wood. The primary wood consists of tracheids with a few parenchyma cells and measures about 2.5 mm. in diameter. Other than fragmentary pieces of the cortex, no tissues are preserved outside the xylem. These two steles are arbitrarily designated *A* and *B* for the purpose of identification in this description.

The two steles remain unchanged until about midway through block *D,* at which point (text fig. 5-2) a stele departs from *A.* Another small separate stele may also be noted here; this and several others were observed in a peripheral position and were not traced to an attachment with *A* or *B*; lack of attachment is due apparently to faulty preservation. At a slightly higher level, midway through block *E,* several branch steles are now evident (text fig. 5-3). These represent additional branches from *A* and *B* and the divisions of branches themselves.

It will be noted from the text figures as well as the photographs that many of the steles are only partly preserved. Most notable is the gradual loss of stele *A.* The preservation is poor at the level shown in text-fig. 5-3; at the level of text-fig. 5-5 only half of it is present, and by the time block *J* is reached (text-fig. 5-7) it has disappeared. Stele *B* retains essentially the same size and form through the specimen and is at all times dominant in relation to its branches; it seems likely, judging from the portion of it that is preserved, that stele *A* followed the same pattern. The preservation in block *H* is very poor, and little of significance remains beyond block *J.*

For the most part, the branch steles shown on the left side of the text-figures come from stele *A* and those on the right side from stele *B.* A union of the two "systems," however, is evident in text-fig. 5-6 in the form of the elongate stele in the upper part of the figure.

The maximum number of steles present at any one point can be determined only approximately, because of faulty preservation and in part because of the prolific anastomosing nature of the system. For example, in text-fig. 5-6 a more

Text-fig. 5. *Medullosa heterostelica.* Transverse diagrams of specimen No. 819 showing changes in the stelar form through blocks C–J (see text-fig. 4). Several of the poorly preserved steles are omitted. 1, C-t2; 2, D-t17; 3, E-t14; 4, F-t16; 5, F-t9; 6, G-t1; 7, J-t1.

or less 7-shaped stele may be noted encompassing the right side of the figure, whereas 16 mm. above (text-fig. 5-7) this has divided into five or six steles. At the latter point, which may be taken as representative of the more highly divided part of the stem, there are about fourteen whole or fragmentary steles.

So poorly is the stem preserved beyond block *J* that we are unable to determine whether or not it passes back into the two-stelar phase as reported for the type specimen. The lack of cortical tissues and petiole bases also makes it impossible to determine which steles contribute directly or indirectly to the petiole trace system.

The only previously described *Medullosa* specimen with which this may be compared closely is *M. heterostelica*. As stated above, it differs most notably in size, the two central steles being twice as great in diameter as those of the type specimen. Assuming that the multiple stelar condition in our specimen is also a nodal region, the size contrast is comparable here. This region is described as being approximately 5.5 cm. long in the type specimen (Stewart and Delevoryas, 1952, p. 508, figs. 5 and 12). In our specimen the multiple-stelar phase starts in block *D* and runs through *J*, a distance of 9.3 cm., and undoubtedly ran for several centimeters more if indeed it did again assume the two-stelar phase.

Aside from the size there is nothing on which to base a specific difference, and for that reason our specimen is assigned to *M. heterostelica.*

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

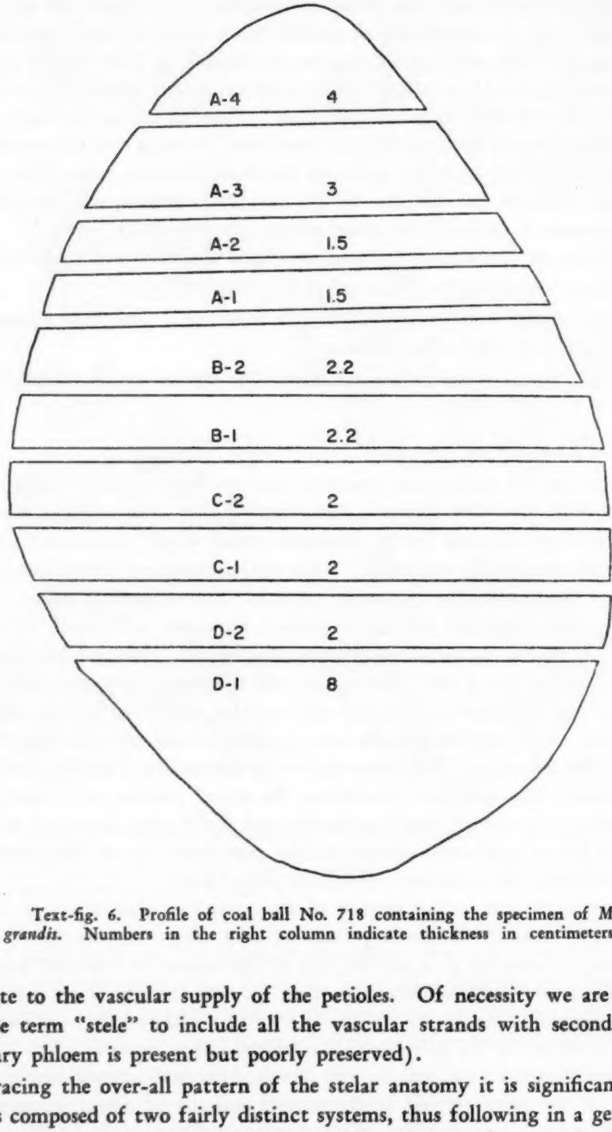
MEDULLOSA **grandis** sp. nov.

The most unique medullosan specimen that we have acquired in recent years is No. 718 from the West Mineral, Kans. locality. It is especially interesting by virtue of its large size and by its numerous steles which anastomose freely and present much anatomical variation. With the exception of *Medullosa noei* it is much larger than any of the previously reported Carboniferous species.

The specimen composes the major portion of a coal ball about 30 cm. long and 28 × 12 cm. in its largest transverse dimensions. The coal ball tapers to a very blunt point at the *A* end (text-fig. 6) and the stem decreases correspondingly in size; that is, the decrease is normal and not due simply to loss of part of the stelar system. This small end is also heavily pyritized and less well preserved than the rest of the specimen. The other end is represented by a broken surface. If, as seems likely, this specimen constitutes the apical portion of a stem, then it clearly represents a tree of some magnitude; and if the stem continued to increase in diameter for an appreciable distance at the rate shown in our fragment it must have soon attained the dimensions of a large forest tree.

In order to present a clear picture of the complex organization of the stelar system a restoration of the major portion of it is shown in text-fig. 7. This is accompanied, in text-fig. 8, with diagrams of the system at the four points indicated. All the numerous smaller steles that show in text-fig. 8 are not included in the restoration (text-fig. 7). Text-fig. 6 is a profile of the coal ball, which may be referred to for the position of the text and plate figures.

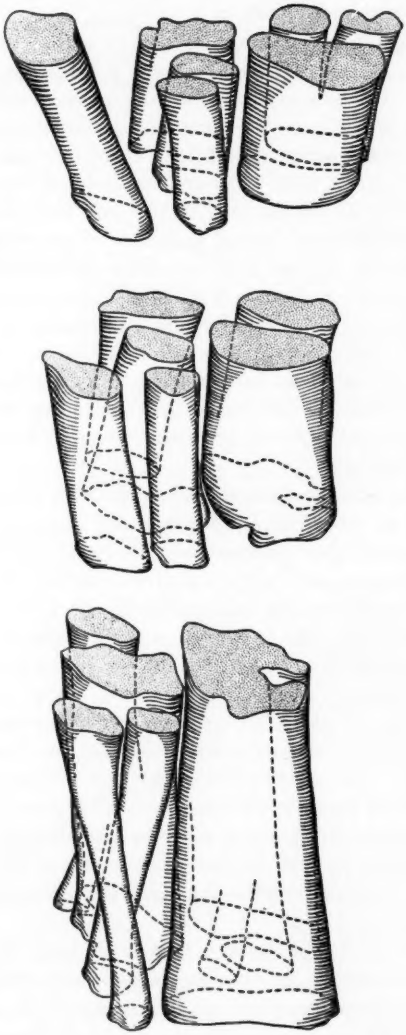
A casual glance at the text-figures reveals considerable variation in the size and shape of the steles as well as the relative amount of primary wood that is present. A striking feature is the great variation in the structure of the secondary wood itself, in which the different ratios of parenchyma and tracheids present distinctly atypical steles. It is of course likely that many of the smaller strands



Text-fig. 6. Profile of coal ball No. 718 containing the specimen of *M. grandis*. Numbers in the right column indicate thickness in centimeters.

contribute to the vascular supply of the petioles. Of necessity we are therefore using the term "stele" to include all the vascular strands with secondary wood (secondary phloem is present but poorly preserved).

In tracing the over-all pattern of the stelar anatomy it is significant to note that it is composed of two fairly distinct systems, thus following in a general way the type of organization described for *Medullosa heterostelica*. Stelar branching and fusion take place so rapidly that the system presents an intricate anastomosing network. The block is so large that it did not seem practicable to run a complete



Text-fig. 7. A restoration of the stelar system of *Medullosa grandis.*

series of sections through the specimen. Text-fig. 7 presents, therefore, a slightly less complex picture than that actually represented by the number of steles involved and the branching pattern.

The numbers assigned to the individual steles in text-fig. 8 *A–D* are arbitrary and are intended to facilitate following the steles through the portion of the stem that is represented. It seems somewhat simpler to start with the smaller end, presumably the apex of the stem. We may first follow the course of steles 1, 2, and 3 from *A* to *B*, where steles 1 and 2 have fused and stele 3 is evidently preparing to divide. In *C* the three steles are shown fused into a single irregular-shaped stele. Finally in *D* this has now divided into four distinct steles. These fusions and divisions take place through a distance of approximately 10 cm.

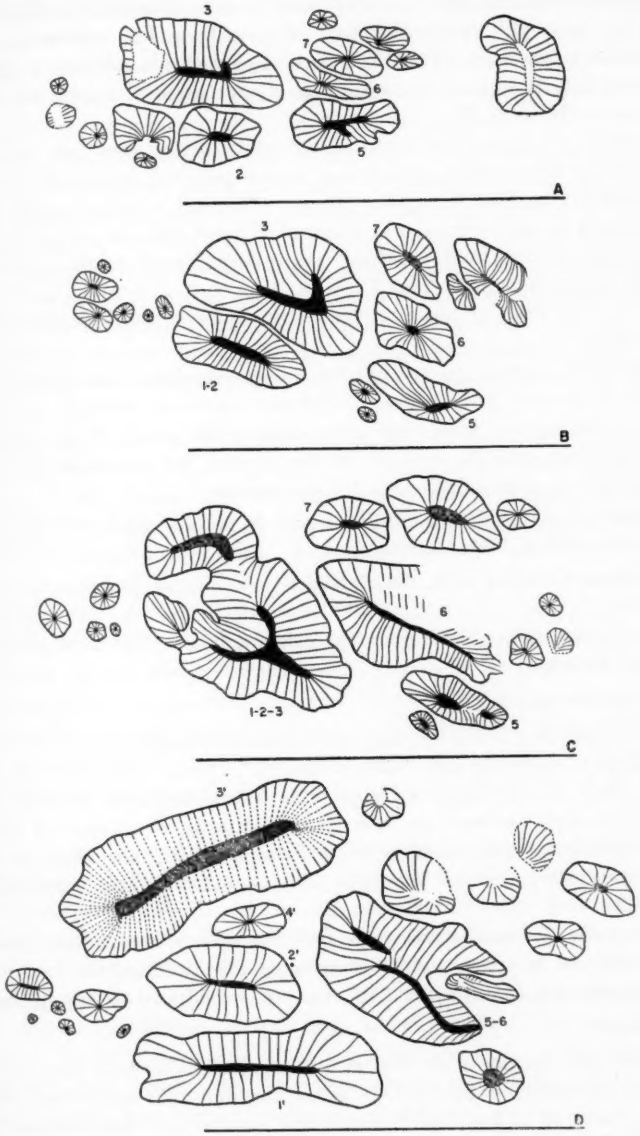
Returning to text-fig. 8-*A* we may now trace through the second "system" of steles, represented here by numbers 5, 6, 7; these also increase markedly in size in passing through *B* to *C*. Because of faulty preservation it was not possible to interpret precisely the changes that ensue below this point. At least one branch stele departs from number 5, and in *D* steles 5 and 6 are fused to form a very irregular-shaped wood mass. There can be little doubt that the numerous smaller steles shown to the right are a part of this stelar "system," but they have not been traced in actual connection.

In addition to the more conspicuous steles considered above there are numerous smaller ones all of which display a remarkable range of variation in their organization. Certain of these features may now be considered.

Figure 13, which represents a single stele from the cross-section shown in fig. 1, may be taken as typical of the organization of the larger "normal" vascular elements of the stem. The stele is slightly crushed, although it is evident that there was no great abundance of primary wood. In fig. 14 is illustrated a portion of another stele of generally comparable dimensions. It is evident here that the primary wood is composed chiefly of tracheids with little admixed parenchyma. There is nothing exceptional about the organization of the secondary wood of the stele shown in fig. 13. The pitting in the radial walls of the tracheids is typically pteridospermous, and the rays are rather narrow and of great height.

Several of the larger steles compare with the one described above, but others vary much in their course through the stem with respect to the relative abundance of parenchyma and tracheids, and this difference may be noted in both primary and secondary wood.

Figure 16 shows a portion of the large stele at the upper right of fig. 1. The central region of this stele is occupied by parenchyma exclusively, whereas the immediately surrounding secondary tissue consists chiefly of parenchyma with a few radially aligned rows of tracheids, a feature that is common in the secondary xylem of some of the large Permian Medullosas. Toward the periphery of the stele the organization compares closely with that observed in the stele shown in fig. 13. It should be kept in mind here that the stele shown in fig. 16 is directly connected with the "normal" stele shown in fig. 13.



Text-fig. 8. *Medullosa grandis.* Transverse diagrams of specimen 718 showing changes in the stelar form through blocks A–C (See text-fig. 6). A, A-t2; B, B2-t1; C, B1-t1; D, C-t1.

Another predominantly parenchymatous stele is illustrated in fig. 15. Here there is a large pith composed chiefly of parenchyma but with some groups of tracheids scattered through it. The tracheid-parenchyma cell ratio in the secondary wood is variable, as is indicated in the figure. A small branch stele preparing to depart is shown at *B*.

Most of the extra-stelar tissues of the specimen have been lost, but the fragments of the characteristic medullosan internal periderm suggest the enclosure of the stelar system here as in other species. There is a rather poorly preserved groundwork of parenchyma, and scattered through this are numerous secretory canals, each enclosed by a "periderm" ring. Several small traces are present, also enclosed in the same tissue (fig. 8).

There is no evidence suggesting that any portion of this specimen represents a nodal region.

Diagnosis: Stem large, greatest known traverse dimensions of the stelar system 12 $\times$ 28 cm. Steles numerous (18–20), extremely variable in size (up to 6 cm. in diameter), shape, and xylem-parenchyma ratio. Steles anastomosing frequently, but generally arranged in two systems, one somewhat more complex than the other. Extra-stelar organization unknown.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

Type specimen is deposited in the Paleozoic plant collections of the U. S. National Museum.

Medullosa noei Steidtmann

Our recent coal-ball collections from southern Illinois include two specimens of the large tri-stelar *M. noei* (Steidtmann, 1937, 1944). They are approximately 43 cm. and 30 cm. long; although this is intended only as a preliminary account, since the two have not been studied critically, they appear to follow the general stelar pattern described above for *M. thompsonii*. They show no evidence of the multiplicity of stelar branching and fusion found in *M. heterostelica* and *M. grandis*.

One of the specimens showing the complete stelar system is illustrated in fig. 18; the original specimen was a fragmentary one, although the concept of its stelar organization (Steidtmann, 1937, fig. A) is confirmed by our specimens.

Discussion:

Several contributors to the literature on the Medullosas have been tempted to speculate concerning the relationships of the now numerous species included in the genus. A total of no less than 44 species and varieties have been recorded to date, and since the stelar anatomy is nearly as diverse as the number of entities recorded it is understandable that paleobotanists find it intriguing to propose evolutionary lines in the group. Although the primary purpose of this paper is to present

what appear to be significant factual contributions, a few speculatory comments seem to be in order.

One point of anatomical significance is well illustrated by the assemblage of specimens discussed in this paper, namely, the contrast in the relative constancy of stelar number among certain of the better-known species.

Medullosa endocentrica Baxter may be taken as a striking example of a species in which the stelar number remains constant. The single available specimen was some 12 cm. long, a significant length considering the small diameter of the plant. In this specimen the tri-stelar form remains constant throughout its length, there being no evidence of stelar fusion, division, nodal complexities, or notable changes in shape or size of the individual steles. Based on observations of a specimen some 23 cm. long, *M. thompsonii* also displays a relatively simple stelar pattern. There is some stelar division and fusion; this, however, is not apparently related to the position of the nodes, and the number of steles varies only from two to three (text-fig. 2).

The stelar complexity of *M. grandis* and *M. heterostelica* presents, at least on casual observation, a striking contrast to the organization found in *M. endocentrica* and *M. thompsonii.* The contrast may cause one to question the inclusion of all four species within one genus. The complex stelar form of *M. grandis* and *M. heterostelica* does, however, mask an apparently basic pattern of organization. We have demonstrated that, so far as preservation allows, our specimen of *M. heterostelica* contains a two-stelar system. That is, the two "original" steles each divide profusely, but the two resultant groups of steles remain more or less distinct. In *M. grandis,* also, the stelar system appears to be organized into two groups, although we are unable to determine whether or not the specimen at our disposal represents a nodal region comparable with that of *M. heterostelica.* In view of the rather significant size of the specimen of *M. grandis,* it seems likely that the stem did not possess the two-stelar internodal simplicity of *M. heterostelica.*

One point can be stated with certainty concerning the interrelationships of the Medullosas is that we can guess, and guess only vaguely, concerning possible lines of development. The extent to which competent workers have disagreed in their concepts of racial development in the genus is indicated by comparing the phyletic chart of Baxter (1949, p. 309) with that presented by Stewart and Delevoryas (1952, p. 514). In the latter, *Sutcliffia* is assigned a basal position, whereas Baxter suggests that *Sutcliffia* represents a specialized side branch from a *Medullosa* of the *M. anglica* type. It is also significant that the discovery of *M. heterostelica* caused Stewart and Delevoryas (1952) to modify rather radically the concept presented in Stewart's earlier paper of 1951.

It is thus evident that the discovery of each new species of *Medullosa* may result in a new phyletic scheme for the genus, particularly in view of the unique specimens that have been discovered in recent years. Our feeling is that inter-

relationships within the genus are actually much more complex than has been implied by previous workers. Evidence in support of this view is contributed by the recent report of *M. olseniae* from the Permian of Texas (Roberts and Barghoorn, 1952). It is a multi-stelar stem, the steles being arranged in a peripheral group resembling *M. leuckarti* or *M. solmsi*, but subsidiary steles are reported to be lacking. It is thus difficult to "fit" it into the top of either of the two branches of the genus indicated in the chart presented by Stewart and Delevoryas.

Although we shall refrain from commenting further on the evolution of the genus as a whole, we should like to conclude with a comment on the type of anatomy presented by the *grandis-heterostelica* complex. It has been assumed by many previous workers that the Medullosas evolved from a single-steled plant of the *Heterangium* type or one in which a single stele appears dominant, as in *Sutcliffia*. Referring for the moment to the type of anatomy exhibited by *M. grandis*, there appear to be at least two possible explanations for its origin:

First, in view of the two distinct stelar "systems" represented, *Medullosa grandis* may be considered as having evolved from a *two-stelar* ancestor with stelar proliferations resulting in this type of multi-stelar stem. Further modifications of the *M. grandis* pattern may then have resulted in the diverse types found in the Permian. Then, unless we assume a *phyletic return* to the two-stelar form, *M. grandis* may be considered as an advanced species having evolved from the *anglica-thompsonii-distelica*-etc. group. Stratigraphic relations are not very helpful here. The exact position of *M. grandis* in relation to the species cited above is not known, but it seems likely that *M. anglica* is of earlier origin, while *M. thompsonii* and *M. distelica* are of later origin (see Andrews, 1951, p. 433).

Second is the possibility that *M. grandis* is a distinctly *primitive Medullosa* in which we may see the beginnings of dominance being assumed by a few steles. In this case *M. heterostelica* may represent a species in which the multi-stelar phase is confined to the nodal region and in turn the two- to three-stelar species have evolved (as suggested by Stewart and Delevoryas) by the complete loss of the multi-stelar phase. This suggestion next requires some tentative explanation concerning the origin of *M. grandis*, and it is at this point that we would diverge most radically from previous views.

In recent years several poly-stelic plants have been reported from Devonian and lowermost Carboniferous horizons such as *Xenocladia* (Arnold, 1952), *Pietzschia* (Gothan, 1927; and Read and Campbell, 1939), *Steloxylon* (Solms-Laubach, 1896, and Read and Campbell, 1939), and *Cladoxylon* (Bertrand, 1935). It is not implied that *M. grandis* may be traced directly to any of these plants, but it is suggested that such a stem *type* may represent a medullosan ancestor.

Acknowledgement:

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Explanation of Plate

PLATE 16

Fig. 1. *Medullosa grandis* Andrews & Mamay. Transverse section, peel 718-C-tl. Natural size.

1.

ANDREWS and MAMAY — AMERICAN MEDULLOSAS

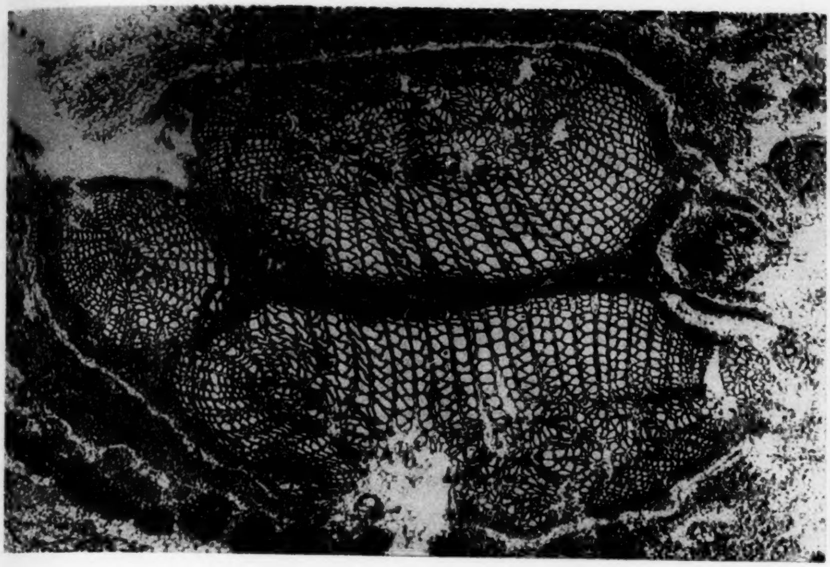
Explanation of Plate

PLATE 17

Medullosa thompsonii Andrews

Fig. 2. Transverse section of stelar system of specimen No. 721. Peel 721-B-b2. × 14.

Fig. 3. Transverse section of a single stele of specimen No. 713. Peel 713-D2-t4. × 8.



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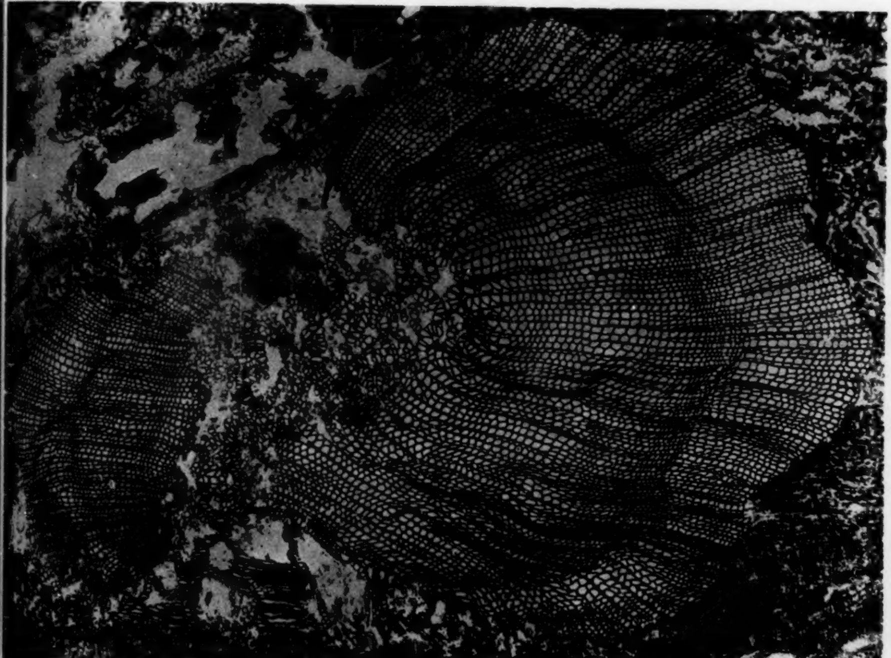

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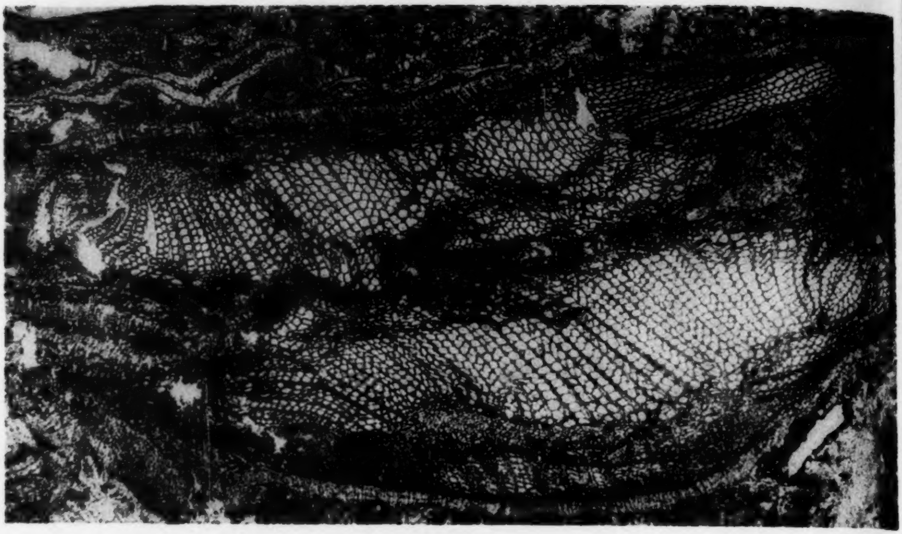
ANDREWS and MAMAY — AMERICAN MEDULLOSAS



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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 18

Fig. 4. *Medullosa distelica* Schopf. Transverse section of stelar system of specimen No. 688. Peel 688-A-t13. × 15.

Fig. 5. *Medullosa thompsonii* Andrews. Transverse section of specimen No. 713 showing two-stelar phase. Peels 713-D2-b3 and 713-D1-b3. × 4.

Explanation of Plate

PLATE 19

Medullosa thompsonii Andrews. Transverse sections of stelar system.

Fig. 6. Peels 713-A1-1,b2 and 713-A2-1,b2. × 4.

Fig. 7. Peels 713-B1-b7 and 713-B2-b8. × 4.

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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS


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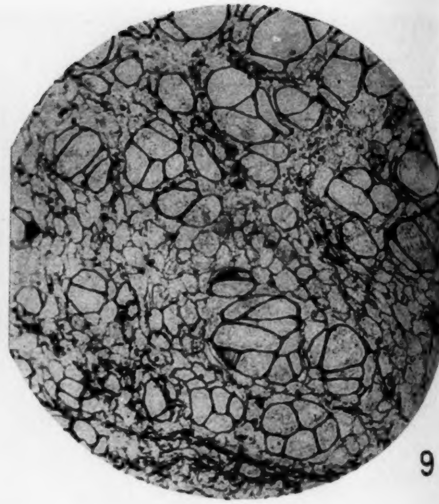
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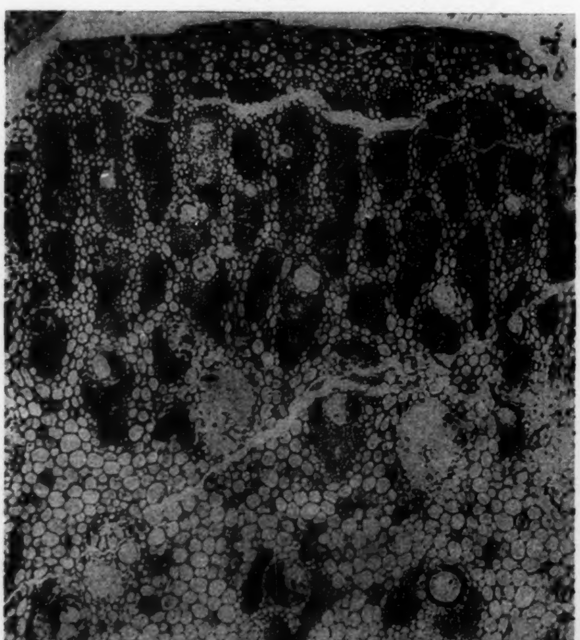

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ANDREWS and MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 20

Fig. 8. *Medullosa grandis.* Transverse section of a small vascular strand, presumably a leaf trace, surrounded by "periderm." Peel 718-B1-t1. × 55.

Fig. 9. *Medullosa distelica.* Transverse section of primary wood. Peel 688-C-b2. × 60.

Fig. 10. *Medullosa distelica.* Transverse section of the outer cortex of the petiole. Peel 688-B-t13. × 25.

Fig. 11. *Medullosa heterostelica* Stewart and Delevoryas. Transverse section showing the two-stelar phase. Peel 819-B-t3. × 2.4.

Explanation of Plate

PLATE 21

Fig. 12. *Medullosa heterostelica.* Transverse section of the stem showing the multi-stelar phase. Peel 819-G-t3. × 3.

12

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

13

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ANDREWS and MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 22

Medullosa grandis

Fig. 13. A single stele. Peel 718-C-t2. × 3.

Fig. 14. Portion of a single stele showing primary wood. Peel 718-B2-t1. × 6.5.

Explanation of Plate

PLATE 23

Medullosa grandis

Fig. 15. A single stele showing parenchymatous primary and secondary wood. Peel 718-C-t2. × 7.

Fig. 16. Portion of the secondary wood of a large stele showing high ratio of parenchyma. Peel 718-C-t2. × 8.5.

15

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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

17

18

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 24

Fig. 17. *Medullosa distelica.* Transverse section of portion of a petiole. Peel 688-A-t4. × 5.5.

Fig. 18. *Medullosa noei* Steidtmann. Transverse section of stelar system. Peel 687-B-t1. × 0.9.

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THE DISTRIBUTION OF *DIOSPYROS VIRGINIANA* L.*

HARRY R. SKALLERUP**

While the factors responsible for the present distribution of *D. virginiana* are in themselves not unique, the study of the literature pertaining to the native persimmon is particularly rewarding. Because the persimmon is both a fruit and forest tree the information obtained is increased two-fold. The combination of botanical, horticultural, and dendrological data answers some of the questions in regard to the determination and interpretation of the many aspects of its life phenomena. An attempt will be made here to present the factors affecting the macro- and micro-distribution of *D. virginiana* and to review and supplement certain aspects of the literature relating to them.

The genus *Diospyros* has a fossil record extending to the Mid-Cretaceous Era, and is represented by leaves, wood, calices, and even fossilized fruit, each having been reported from various locations throughout the world. Species evidently grew in Greenland, Siberia, Canada, northern Japan, Alaska, the British Isles, and in North Africa and Arabia (Berry, 1923). Although no major geographic region of the United States is without one or more fossil representatives of this genus, only one, based upon wood from a Pleistocene deposit in Louisiana, has been designated *D. virginiana* (La Motte, 1952). Yet it is reasonable to assume, in the light of leaf variation evident within the extant species, that perhaps a few others of the North American forms based on leaf remains and present as far back as the Cretaceous (Berry, 1923) may also be *D. virginiana.* Indeed, the present distribution pattern of *D. virginiana* indicates a very long history. In common with other plants of chiefly tropical affinity, it appears to have been dispersed throughout eastern United States from ancient centers in the Appalachian-Ozark highlands (Fernald, 1931).

Diospyros virginiana is now known only from the United States, and occurs within the area depicted in fig. 1. Each dot represents a county from which a collection has been reported. The apparent low density of collections in the Southeast can best be accounted for by a lack of records from this area. Thus, although only a few collections are represented from Mississippi, Alabama, and Louisiana, floras of these states list *D. virginiana* as occurring throughout the area. Moreover, a survey of the commercial stands of persimmon timber in the United States showed these states to be especially well represented (Fletcher, 1915). The critical collections at the periphery of its range are likely to define its extent fairly well, since specimens representing the rare species and new range extension are collected with a frequency disproportionate to their occurrence in the natural vegetation.

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*This paper is a portion of a monograph on the native persimmon, presented as a master's thesis in the Henry Shaw School of Botany of Washington University. Most of the bibliography of the original thesis has been retained since it includes some references not generally available.

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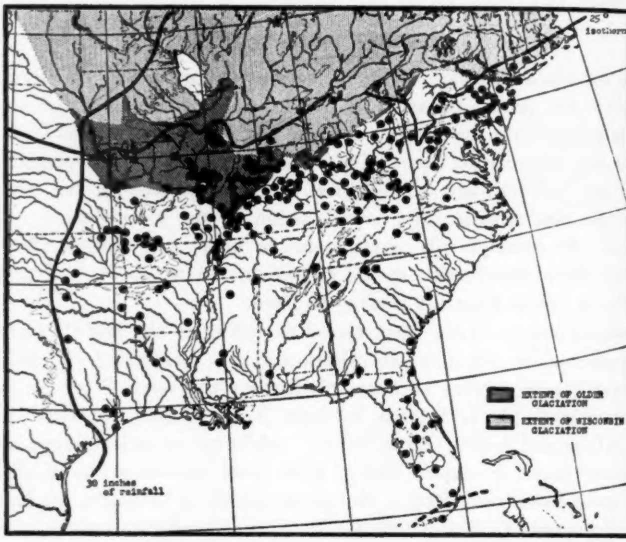

Fig. 1. Range of *Diospyros virginiana* L. Glacial and climatic boundaries drawn after Flint (1945) and Kincer (1922, 1928), respectively.

The study of the distribution of a tree such as *D. virginiana* has its disadvantages as well as its advantages. Specimens may be reported or collected from trees introduced outside the natural range, and although the trees may be hardy in these sites they could not have survived in nature as seedlings. Also, reports of non-fruiting specimens, particularly in the older horticultural accounts which ascribe non-fruiting to cold temperatures, may be erroneous due to the fact that *D. virginiana* is dioecious and some of the trees in question may be staminate.

Diospyros virginiana is found growing widely in areas of older glaciation (the Nebraskan, Kansan, and Illinoisan) and in the unglaciated area of the South. In the north and west of the older glaciated area *D. virginiana* appears to be limited by temperature and rainfall, respectively. Few specimens were found north of the 25° F. February isotherm as determined by Kincer (1928)[1]. Inasmuch as individual trees transplanted north of the 25° isotherm are able to survive and bear fruit, it seems that the photoperiod is not a factor in flower formation, and therefore does not limit its distribution (Naudin, 1880; Harrington, 1900; Trabut, 1926; Baldwin and Culp, 1941). It is possible that seedlings in the wild are unable to withstand the cold and to become established in such areas. This is supported by the report of Aikman and Boyd (1941) that persimmon trees planted for soil con-

[1]Of the series of maps prepared by Kincer (1928), February represents the coldest winter month for a period of 20 or more years.

servation purposes in southeastern Iowa (at the northwest limit of the range) needed a protected site if they were to survive.

In determining which factors might account for the western limits of the species, two possibilities appear: both the line of 30 inches of annual precipitation and an increase of 1000 feet in elevation running northward from the Edwards Plateau coincide fairly well with the distribution of *D. virginiana*. Since the persimmon is found commonly in the southern Appalachians (Eddy, 1927), it is more probable that the rainfall is limiting. (In the more northern mountains of Pennsylvania and West Virginia, persimmon is reported to be more rare than in the lowlands—letters from J. A. Small, E. L. Core—but here the lower winter temperatures and high elevations are probably responsible.) While it is not known at which phase of its growth the moisture requirement may be critical for *D. virginiana*, in other fruit trees it has been found that an annual precipitation of at least 30 inches is required by mature individuals (Magness and Traub, 1941).

While temperature and rainfall thus appear to limit the greater part of the range of *D. virginiana*, there is a conspicuous absence of specimens from the area of the last or Wisconsin glaciation within the compass of the 25° isotherm. That this area does not differ significantly in climate fails to explain the absence of *D. virginiana* in the later glaciated region. Berry (1923) states that during Pleistocene times the native persimmon retreated far to the south of the ice front, only to spread north again in the "wake of the ice sheet." With regard for the dangers in assuming that post-glacial expansion is still going on (Deevey, 1949), it would appear that *D. virginiana* had advanced into the glaciated area, only alternately to withdraw and advance in response to the Wisconsin glaciation, so that now it occupies the northern boundary of the older glaciation (where it is not limited by low temperatures) and has made but slight advances into Indiana, New Jersey, and Connecticut, the areas of the more recent glaciation. The isolated specimens in Indiana, Ohio, and New York (fig. 1) probably represent collections from cultivated trees, as does a specimen from Massachusetts (not shown on map—letter, R. Rollins, 1953).

Baldwin and Culp in 1941 made a cytological study of persimmon from selected stations throughout the range and found that two chromosome races are present: $2n = 60$ and $2n = 90$. Considering other members of the genus (Table I) it appears that the basic number of chromosomes is 15; accordingly the races of *D. virginiana* are regarded by Baldwin and Culp as tetraploid and hexaploid. Their relative distribution is interesting: the 60-chromosome race has a continuous distribution in the central and southeastern parts of the range, while the 90-chromosome race occupies a peripheral position throughout the rest of the range.

Several additional counts were made in this study. Collections of seeds gathered in St. Louis, Franklin, and Bollinger counties in Missouri, and from Washington County, Arkansas, were grown in the experimental greenhouse at the Missouri Botanical Garden. Chromosome counts made from aceto-lacmoid root tip squashes

TABLE I

SUMMARY OF KNOWN CHROMOSOME NUMBERS IN *DIOSPYROS**

Species	2 n	Source
D. discolor	30	Namikawa, Sisa, and Asai (1932)
D. texana	30	Baldwin and Culp (1941)
D. lotus	30	Namikawa and Higashi (1928)
D. kaki	90	Namikawa and Higashi (1928)
D. virginiana	60, 90	Baldwin and Culp (1941)

*After Baldwin and Culp, 1941.

showed these to have 90 chromosomes—the number reported by Baldwin and Culp in Crawford County, Kans., and Jasper County, Mo. While it would be premature to draw conclusions as to the meaning of the chromosome races in this species, it is of interest to note that the 60-chromosome individuals are found in and about the ancient eastern center of the species. The occurrence of higher polyploids on the periphery of the range is subject to two interpretations: (1) that they are autopolyploid derivatives which have been able to colonize areas not so accessible to the lower polyploid (Cain, 1944; Stebbins, 1950); (2) that the 90-chromosome race is actually of hybrid origin (with an extinct species or race) and is spreading eastward along the northern boundary of tetraploid *D. virginiana*. In either case, studies of both the morphology and cytology of plants of known chromosome number will be required before the question can be answered even tentatively.

In the course of horticultural practice *D. virginiana* has been introduced into climates outside of its natural range with varying degrees of success. It had been introduced into England before 1629. Parkinson's 'Paradisi in Sole Paradisus Terrestris' gives the first account of cultivated persimmon trees *(Lotus virginiana)*. One specimen given to George III by the Duke of Argyle (ca. 1790) and grown in the old Kew Arboretum was of considerable dimensions in 1895. At that time it was "apparently as contented [there] as in its native habitat" (For. and Gard., 1895). *Diospyros virginiana* has also been grown successfully in British Guiana (Hiern, 1873); it fruits regularly in the warmer European climates, although it is irregular in more severe climes where it has been reported to withstand temperatures as low as —25° C. (Naudin, 1880; Trabut, 1926).

FACTORS AFFECTING LOCAL DISTRIBUTION

Although the persimmon is frequently cited in the literature as a pioneer species —a tree that is among the first to grow in almost any situation—a survey of the flora growing spontaneously within the present city limits of St. Louis failed to show any persimmon trees growing in those abandoned places where a "pioneer" would be expected. That persimmons did grow in the area now incorporated as St. Louis proper is borne out by a few, but reliable, references. One of the most

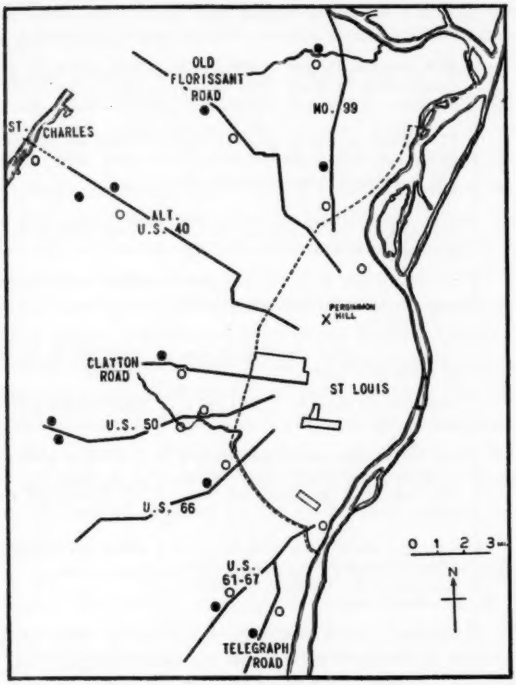

Fig. 2. Map showing occurrence of *D. virginiana* in the St. Louis area. Black dots represent sites where it was found closest to the city; circles represent apparently favorable sites where it did not occur.

interesting is the narrative by Elizabeth Kennerly Russell, 'Persimmon Hill'. Although written in the style of a saga, its title refers to the actual Kennerly mansion, *Côte Plaquemine*, built in 1832 on a hilly tract of land "five miles northwest of town . . . where Taylor and Kennerly Avenues cross today," and named for the persimmon trees commanding the site (Russell, 1948). Prior to this time the land outlying St. Louis that was not upland forest had been kept in prairie by the Indians who annually burned the vegetation in order to flush out game. By 1836, the prairies had practically disappeared, due to the cessation of the autumnal fires and were succeeded by young forests (Beilmann and Brenner, 1951).

Nicholas Riehl, collecting in 1838, gathered persimmon specimens from the "fôrets" of St. Louis; while a visiting farmer, Patrick Shirreff, tasted his first persimmon upon travelling Old St. Charles Road, only to mention its disagreeable taste in a letter written home, dated 1835 (Stevens, 1906). Coincidental in time and place with references to the flora are necessarily those to the birds and animals of the region about which William Kennerly reminisces ". . . we learned the ways

TABLE II

Road	Sites where *D. virginiana* was found (represented by black dots, fig. 2)	Sites where *D. virginiana* was not found (represented by circles, fig. 2)
I. U.S. 61	(1) Clone, on top of slope at edge of old field with 5, 7* (2) Individuals in grove with 2, 4, 8	Mixed oak association
II. Telegraph Road	Scattered, on top of ravine, s.w. side in mixed oak woods	Flood plain of Mississippi River
III. U.S. 66	(1) Clone, same as I (1). (2) Scattered, in grove with *Pinus echinata*, 1, 2, and 6	Mixed oak association
IV. U.S. 50	Clone, on slope of old field at edge of grove of *Ulmus*	Along River des Peres
V. Clayton Road	Scattered, in stand of 1, 2, 3, 4, 8, and *Cornus* sp.	Brier thicket in recently cleared field
VI. Alternate U.S. 40	(1) Clone, slope of old field, with 5, 7, *Andropogon virginicus*, *Aster* sp. (2) Individual in mixed oak association	(1) Flood plain of Missouri River at St. Charles (2) Mixed oak association
VII. Old Florissant	Scattered, along ditch with 4, 5, 7, *Rhus glabra*, *Populus deltoides*. Also, specimen of *D. virginiana* var. *pubescens* found here	Mixed oak association
VIII. Missouri 99	Scattered, side of road, with 2, 4, 6, 8, *Rhus glabra*, *Prunus* sp.	Dense grove of *Ulmus* at edge of cultivated field
IX. Missouri 109 (not on map)	Scattered, on glade with *Bumelia lanuginosa*, *Cercis canadensis*	

*1. *Acer Negundo*
2. *Celtis occidentalis*
3. *Platanus occidentalis*
4. *Quercus* sp.
5. *Rubus* sp.
6. *Sassafras albidum*
7. *Symphoricarpos orbiculatus*
8. *Ulmus americana*

of animal life in the woods and meadows . . . we could read the small dainty hoofprints of the deer as well as the bobcat's heavier tread . . ." (Russell, 1948). Wild turkey, deer and abounding game were also written of by Flagg in 1836 (Thwaites, 1896–1901; see also Beilmann and Brenner, 1951, for a more complete account). However, with the expansion of the city, persimmon became scarce within its limits. In 1911 the Engelmann Botanical Club listed *D. virginiana* occurring in St. Louis proper only in such floral sanctuaries as Missouri Botanical Garden and in Tower Grove and Forest parks (Engelmann Bot. Club, 1911).[2]

[2]Unfortunately the origin of these trees, like plants in many parks and botanical gardens, is speculative. Among the trees in the nursery of Tower Grove Park in 1871, fifty were listed as being persimmons (Shaw, 1871). Henry Shaw, in addition to purchasing the Riehl collection of herbarium specimens, also bought the first trees planted in his Garden from the Riehl Nursery (Spaulding, 1909).

Ironically, a year later persimmon was recommended as a native tree suitable for growing in St. Louis (Jensen, 1912).

To determine the present occurrence of persimmon in the St. Louis area, a reconnaissance was made along the main highways radiating from the city. Although every side road could not be followed, and doubtless, in the forced pace of highway traffic, some trees were overlooked, a fairly complete idea of its local behavior was obtained. Figure 2 and Table II summarize the data obtained. It can be seen that persimmon does not occur within the city limits, and is primarily an upland tree which prefers an open drained habitat. *Diospyros virginiana* was usually found growing in clones or scattered in open situations where there is little competition; or else it was found scattered with other second growth trees or in young mixed-oak forests (pls. 25 and 26). In the former instance, the trees were young and were initiating growth, while in the latter instances they were comparatively old or dying and represented the last of their number. The present local absence of persimmon within the metropolitan area can not be explained on the basis of unfavorable habitat brought about by smoke or industrial gases, for trees are successfully grown as ornamentals in the city parks and at the Missouri Botanical Garden. Rather, the lack of dispersal agents for its seeds appears to be the underlying cause.

Persimmon is poorly equipped for dispersal by means other than animals, or, indirectly, by man. The fruit, a true berry, ranges from ¾ to 1½ inches in diameter, and bears proportionately large seeds, four to eight in number. Once separated from the pulp, the seeds are not light enough to be scattered by wind or to float upon water. In the city they can still be seen under cultivated trees, untouched by squirrels, rabbits, or rats, as late as June. Tables III and IV list the animals that eat persimmon fruits in the wild. Although these data do not show diet preferences, the fact that the animals listed do eat persimmon fruit indicates that they act in a large degree as dispersal agents for its seeds, since it is unlikely that the seeds are dispersed by any other means. In addition to the animals listed, the pine mouse will use the seeds as food (Martin, 1951), while the meadow mouse is known to include persimmon and *Bumelia* seeds among its caches, and thus figure in its dispersal (L. G. Brenner, personal communication, 1953). While certain birds eat the flesh or pulp of the fruit, it is doubtful whether any listed in Table III B (except the turkey now rare in Missouri) is able to swallow or void the large seeds. This is in contrast to sassafras (*Sassafras albidum* (Nutt.) Nees), a "pioneer" species which does grow spontaneously within the city, whose fruit and seeds are eaten by birds and thus is scattered more widely than persimmon.

TABLE III

LIST OF ANIMALS AND BIRDS EATING PERSIMMON FRUIT*

Species	Per cent of Diet	
	Southeast	Northeast
A. Animals		
Red Fox	10–25	0.5–2
Gray Fox	2–5	0.5–2
White-tailed Deer	0.5–25	Not recorded
Opossum	2–5	Not recorded
Raccoon	5–10	5–10
Ring-tailed Cat (Texas only)	5–10	———
Striped Skunk	0.5–2	Not recorded
B. Birds		
Wild Turkey	Not recorded	0.5–2
Catbird	Not recorded	2–5
Robin	2–5	Not recorded
Yellow-bellied Sap-sucker	Not recorded	Food item of undetermined extent
Myrtle Warbler	0.5–2	0.5–2
Cedar Waxwing	2–5	Not recorded
Mockingbird	Not recorded	Food item of undetermined extent

* Based upon stomach and crop analyses, droppings, and field observations (after Martin, 1951).

TABLE IV

OCCURRENCE OF PERSIMMON IN MISSOURI WILDLIFE*

Species	Samples examined	Occurrence of persimmon
Deer	348 stomachs	40
Coyote	680 stomachs	51
Red Fox	731 stomachs	31
Gray Fox	251 stomachs	56
Quail	5,472 crops	33
Quail	1,358 droppings (roost)	1

* Prepared from letter, L. J. Korschgen, Missouri Conservation Commission, 1953.

HABITAT TYPES

As mentioned above, *D. virginiana* was found either initiating growth in abandoned places or as a minor element in mixed-oak associations. To interpret its behavior in these habitat types, data will be presented from sites where more complete studies were made.

Old Fields.—Many authors list *D. virginiana* as occurring in clones along roadsides, in old fields, and other waste places (Sargent, 1894; Eddy, 1927; Van Dersal, 1938; Steyermark, 1940). Personal observations were made along roadsides and in old fields at the Missouri Botanical Garden Arboretum, Gray Summit, where

information concerning the history of the land is fairly complete. Here, three patterns of "field invasion" were found to be present. These may be characterized as:

(1) Clonal: trees of varying ages, all of the same sex.
(2) Clonal: trees of almost the same age, all of the same sex.
(3) Scattered: trees of varying ages, both sexes present.

(1). A group of the first type was found in a sloping field, abandoned since 1924, which, except for the eradication of elm, had been allowed to grow wild (A. P. Beilmann, personal communication, 1953). An apparently injured, double trunked tree, near a shallow gully, was the oldest element present (c. 20 years). Growing in association with it were *Andropogon virginicus, Allium* sp., *Panicum*, sp., *Aster* sp., *Solidago* sp., young *Juniperus virginiana, Cornus racemosa,* and *Parthenocissus* sp. In somewhat elongated concentric arcs about the old tree were other persimmon trees of different ages, the younger ones being on the periphery, but more numerous down the slope (pl. 25). Trees old enough to bear fruit showed the single peduncles characteristic of pistillate trees. Upon digging near the bases of several older trees, long horizontal spreading roots[3] connecting the older trees were found at a depth of a foot (pl. 25). Several roots were followed for their entire lengths and were found to branch repeatedly. These gave rise to several small trees, one of which is shown in pl. 25. The diameter of the root remained almost constant (¾ inch) except near the tips, where normal growth occurred. There were no evidences of decay or separation of root branches; nor were the branches themselves chance root grafts. From observations of other sites similar to this one (Table II) it was noted that the advance of the younger trees is usually more rapid down the slope, probably due to the greater development of the root system in this direction, a consequence of gravitational influence or greater soil moisture. Although the aspect of this site was largely clonal, a few of the smaller trees may have been seedlings, since seeds collected here were found to be viable.

(2). The second group was observed along a roadside near an abandoned field of similar history to the one above, except for possible disturbances due to road repairs. Other species growing at this site included: *Rhus glabra, Symphoricarpus orbiculatus, Rubus* sp., *Andropogon virginicus*, and *Rudbeckia* sp., as well as a few very young *Juniperus virginiana* trees. The largest persimmon trees examined here were all essentially the same age (about 15 years). They exhibited the uniform growth characteristics and the same sex of trees vegetatively propagated from a common stock, yet no "parent" tree as in the above situation was present (pl. 26). These trees were also found to be connected by stolons, while some individuals had their own groups of younger trees about them. Seeds found at this location were also viable. It is conceivable that this situation was brought about as a result of the

[3]There are references to persimmons as "stoloniferous" (Sargent, 1894; c.f. also, Holm, 1909). However, a complete description of this condition was not found in the literature. The roots described here did not appear to differ in gross structure from the normal roots.

roots of an older persimmon tree having been accidentally cut into pieces and distributed, so that groups similar to those of the first type were concentrated in this small area. That this is possible is demonstrated by a common horticultural practice in which cuttings of persimmon are made for propagative purposes and vigorous sprouts are obtained from them. Further, decapitated trees have been reported to send up root suckers within two months after being injured (Fletcher, 1915).

(3). On the top of the slope of the same field, but away from the road, a third pattern was found. Here trees of varying ages and forms were scattered in groups. Most of the trees were from 15 to 25 years old, although some seedlings were also found. The trees were both staminate and pistillate, and occurred in sporadic groups over the field. Most groups were composed of two or more trees, although some lone trees were noted. Ecologically, this site is part of the "highway" system used by deer and other animals at the Arboretum (Beilmann, personal communication, 1953). The scattered, but grouped trees closely reflect the way seeds are dropped by animals. Yet it is difficult to account for their non-clonal habit. The most likely explanation is that none of the trees were ever injured to the extent that they began to sucker. No plowing had been done in this field for over 25 years and the trees were not planted out. Injury by cattle grazing (besides trampling) is speculative; there are reports that cattle will not browse persimmon leaves or twigs (presumably because of calcium oxalate crystals and tannins present—Deam, 1932; Van Dersal, 1938); however, they are known to eat the leaves when suitable forage is not available (Brenner, personal communication, 1953), and many wild animals are reported to eat the buds and leaves (Missouri Conservation Bulletin, 1940).

Forest associations.—From observations at the Missouri Botanical Garden Arboretum and in the St. Louis area, persimmon was never found upon a river flood plain (Table II), nor were mature trees ever found in a pure stand. Persimmon is frequently mentioned in the literature as existing in pure stands and as reaching its greatest proportions in the basin of the Mississippi River and along the Wabash River Valley. Ridgway (1882, 1894) and Sargent (1894) are probably the uncited sources for these references. However, a more recent survey of the hardwoods growing in Louisiana listed persimmon as only a minor species in all the habitats in which it was found (Lentz, 1929; Hepting, 1936), while Miller and Tehon (1929) report that no persimmon trees as described by Ridgway are now known in the Wabash Valley. Evidently, persimmon was more of a dominant tree (as were others) in the primeval forest than it is in the second growth timber of today.

That *D. virginiana* is only a minor element in present-day associations is verified by other authors. In the Ozark and adjacent plains region, Steyermark (1940) found *D. virginiana* occurring as a pioneer element on dolomitic glades, as a temporary dominant on bald knobs and bare limestone areas, and, frequently,

initiating oak-hickory associations on the acid substrata of the prairie. However, he did not list it as a member in the building of a flood plain climax, in associations where burning-over had recently taken place, or in drainage regions. Palmer (1921) did not mention *D. virginiana* as a conspicuous element of the flora of the Ozarks. Although Lentz lists the persimmon as growing in both the well- and poorly-drained bottomlands of northeastern and southern Louisiana, it was not mentioned as occurring in the Louisiana swamps or in lands subject to overflow. In the Carolinas, Eddy (1927) found it growing at the edge of alder swamps and on the coastal plain, but again, only as a minor or subdominant species.

This evidence indicates the wide range of ecological situations in which *D. virginiana* is able to initiate growth; yet, because of its slow rate of growth, it is shaded out by faster-growing trees. Brenner (1942, 1952) made comprehensive observations of the mixed oak associations in his environmental and quadrat studies at the Gray Summit Arboretum. An example of the short duration of the persimmon in an open woodland can be found from data reported by Brenner from a quadrat staked out in an oak coppice in 1937. At that time, numerous persimmon and other heliophilous trees were keeping pace in growth with the white oaks, the dominant tree. Since then, the white oaks made considerable growth, with the result that, 15 years later, one-fourth of the persimmons were dead and the remaining ones were in poor condition.

SUMMARY

1. Although formerly members of the genus *Diospyros* ranged far to the north, the native persimmon now appears to be limited in its spread to the north by an annual temperature of 25° F., and to the west by rainfall of 30 inches annually. Within these limits, however, it appears uncommon in the area of the Wisconsin glaciation.

2. Supplementary chromosome counts from Missouri (three counties) and Arkansas (one county) are in agreement with previously recorded determinations.

3. Local absence of *D. virginiana* is attributed to eradication of the trees that were present in what is now the city. Dispersal of seeds is largely through the activities of animals, and for this reason persimmon is not known as a pioneer species within urban limits.

4. Three types of "field invasion" by persimmon in abandoned places are described. The ability of the roots to sucker upon injury accounts for the dense clones often found in these situations, although non-clonal situations also exist.

5. Although persimmon once was known to occur in pure, dense stands, more recent reports indicate that this is now not the case. Throughout its range persimmon is reported as a minor species in older associations.

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Explanation of Plate

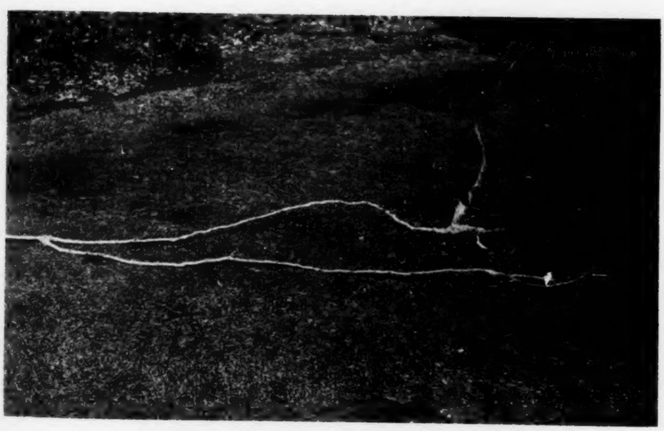
PLATE 25

Diospyros virginiana L.

Fig. 1. Clonal type 1: Trees are of varying ages, and same sex.

Fig. 2. Portion of a "stoloniferous" root from the above situation showing its branching nature and one young tree attached to it. (Length of root approximately 6 feet.)

1



2

SKALLERUP—*DIOSPYROS VIRGINIANA* L.

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2

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SKALLERUP—*DIOSPYROS VIRGINIANA* L.

Explanation of Plate

PLATE 26

Diospyros virginiana L.

Fig. 1. Clonal type 2: Trees are essentially the same age, and are of the same sex.

Fig. 2. Tree group characteristic of the third type.

Fig. 3. Persimmon in mixed oak association.

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WILDWOOD
A STUDY IN HISTORICAL ECOLOGY

ALFRED G. ETTER*

Prologue

This is the story of a gathering of towering trees, old spreading oaks and sky-penetrating hickories that shelter the past in their shade. It is one of the few old woods that remain on the rich uplands that lie northwest of St. Louis between the Missouri and Mississippi rivers. Most of the scattered timber that early settlers found on the headwaters of the creeks in this area was cleared to make fields, or cut for cabins, firewood, fence-posts, lumber, cooperage, or one of the many other purposes for which wood was used during that period of American expansion which so depended on its omnipresence. A few wood-lots, through the smile of fortune, were preserved on tracts of land belonging to large estates. Wildwood was one of these estates, and it took its name from one of these old woods.

History

In the earliest days of the frontier when the land took men and hid them in the shadows of its trees, or lost them on its seas of grass, Wildwood's acres stood ignorant of everything but Indians. Then French forts began springing up along the near-by Mississippi. The French town of St. Louis was founded in 1764. Shortly thereafter Spain assumed control of this Upper Louisiana region. Then near the end of the century the Spanish regime began to yield to the pressure of the American movement west. Grants of land were made by the Spanish to many early frontiersmen and explorers, among them Daniel Boone. Settlements were also recipients. The village of Florissant, a few miles north of Wildwood, received a large gift of land for its common fields and wood-lots, about 1785.

It was around the time of Christmas in 1799 that the Spanish Lt. Governor, Don Carlos Dehault Delassus, granted to John Wendel Engel a tract of 800 arpens (680 acres) lying on the river Maline. Wildwood (to be) was in the northwest corner of this grant, and so first became a parcel in the domain of Man. By 1804 John Engel was apparently stirred by the ever-ready lust for money, for in January he sold 600 arpens of his land to James Rankin for 500 dollars. The other 200 arpens, including Wildwood, he reserved for himself for cultivation. The Spanish regime ended officially in March 1804, and the great territory of Louisiana became American. Whether or not this influenced Engel in some manner is not certain, but in August of that year he completely gave up his ideas of farming by the river Maline and sold to Simon Wood the remaining land, including that destined to become Wildwood. During his brief period of residence Engel had built a house and cleared ten arpens of land and put it under fence. The 200

* Malvern B. Clopton Experimental Farm, Clarksville, Mo. Washington University School of Medicine.

arpens, house, and improvements, together with a spring, went for the price of 200 dollars.

After the transfer of the capital of the Territory of Louisiana to the City of St. Louis, the old fur post became an active and growing city and the headquarters for expeditions and vagrant dignitaries of every description. Simon Wood held his property for sixteen years, but during this time entered into some contract with a gentleman named Josiah McClenahan. Wood could not fulfill the terms, and was obliged in the spring of 1820 to sell his farm to McClenahan for 500 dollars. John Mullanphy had entered into a covenant previously for the purchase of the same land from McClenahan for 750 dollars, as soon as the latter should obtain a clear title to it. This shrewd deal was accomplished just before Missouri received its statehood in 1821.

In 1830 Mullanphy provided that the 200 arpens on Maline Creek should be the property of his young grandson Owen Chambers. It was agreed that should Owen die before the age of twenty-one the land was to revert to Owen's brothers and sisters (of whom there were to be twelve)! Owen did die before he was 21, and in 1850 it was necessary to divide the Maline property. Fortunately Mullanphy had meanwhile procured the 600 arpens of land which were a part of the original grant, so that when the division became necessary there were 800 arpens to be divided among the eight children interested.

To make a complicated story simple, of the resulting eight lots, lots Nos. 7 and 8 contained the 200 arpens of Simon Wood's farm. Lot 7 went to Ellen Chambers LaMotte, wife of J. H. LaMotte, ultimate owner of Wildwood. Lot 8 went to John Chambers, who in 1851 sold the property to LaMotte, and so the original plot of 200 arpens was once more consolidated. The price paid for 110 acres was $3,292.

At the time of the purchase LaMotte was a major in the United States Army and only five years before had been actively engaged in the battles of the Mexican war. He continued his service until 1856, striving assiduously (as he expressed it in letters written at the time and preserved in the library of the Missouri Historical Society) to make the necessary preparations for a happy life on his Maline land. These preparations included the careful sale of many of his investments in property in St. Louis and elsewhere. During this time his farm was run by various tenants, as it had been in the years before it came under his ownership. When he resigned from the army he proceeded immediately with his plans for the transformation of these 220 acres into a home and estate. Work was begun on the construction of his seventeen-room home. Stables, quarters for slaves, and miscellaneous buildings slowly began to rise from mere vision to the reality of Wildwood, country estate of J. H. LaMotte.

Then came the interruption of the Civil War and its attendant complications. Actually it was not until 1867 that the LaMotte family was established in the new home. At that time LaMotte, visiting in Georgetown, received a letter from his son, Frank, to the effect that "We are well and comfortably fixed at Wildwood,

plenty to eat, drink and smoke. Carpets down, potatoes all in, fences up. Harry and mother ride out frequently and enjoy the country very much . . . Uncle is furnishing our apartments in princely style—marble mantels, paper etc."

It was in keeping with the wishes of Major LaMotte that the woods around the house were never cut, though horses, cows and sheep grazed at various times through the undergrowth. Meadows of timothy and fields of corn occupied the flat valleys north of the river Maline. On fertile slopes tobacco was planted and nearer the house were peach orchards, rows of potatoes, and sun-filled patches of watermelons for which the Major became famous. The raising of horses became his particular pastime, and their grazing, combined with that of the sheep and cows, soon made a spacious park from the woodland about the home.

The Victorian refinement of the secluded Wildwood home held sway in luxurious comfort, peace and plenty while Major LaMotte lived. After his death in 1892, his wife and few remaining members of his family continued to live in the home, but his many activities were no longer attended. A tenant farmer ran a few cows in the extensive pastures, but apparently not enough to keep many young trees from sprouting. In 1911 Mrs. LaMotte died and the property went to her daughter, who passed away within a month. Her husband lived alone in the mansion for a few years, leading an almost hermit-like existence, neglecting the home and the fields. At his death, the home stood alone in the woods, forgotten except by vagrants who found the old place a haven on winter nights. There was no caretaker and no interested heir.

In the meantime a new tenant farmer had moved on the property and began building up his dairy herd. According to his recollection, about 1920 he found it necessary to enlarge the available pasturage. Portions of the woods that had grown scrubby were cleared, and the really dense areas in the valley that had never been pastured at all were also cleaned out. Fallen trees and logs were burned, and the cows turned in to finish the work. Mr. S. still resides on the acreage and pastures his cows in Wildwood.

Until 1929 the LaMotte mansion at Wildwood remained abandoned. At that time it was sold to the present owner who removed seven rooms and restored the rest. His purchase included only that land in the immediate vicinity of the house. The remainder (about 200 acres) was sold at public auction in 1934 for $60,000. The purchaser intended to build a private home on the grounds, but his plans did not mature, and during 1946 a "For Sale" sign went up, offering 180 acres for $180,000! The price of this land had thus risen from approximately $1 an acre in 1804, to $3.00 and then $4.50 in 1820, $30.00 in 1851, $300.00 in 1934, and $1000.00 in 1946. Once it was free!

The pressure of suburban development has finally risen to the point where Wildwood can scarcely hope to exist longer as a unit, much less as a farm, within city limits. In this respect, this study is essentially an obituary.

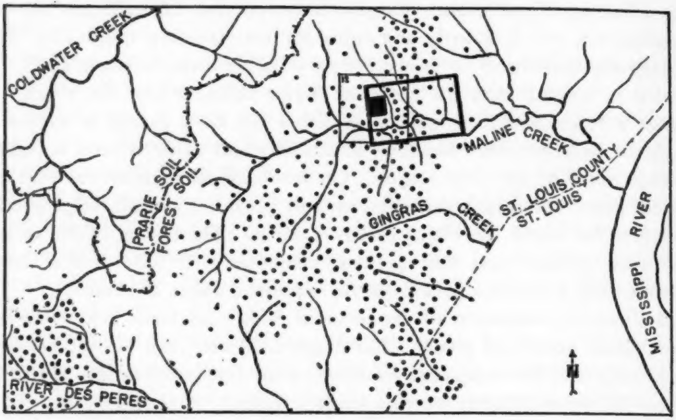

Fig. 1. Prairie and timber areas northwest of St. Louis as recorded by surveyors in 1817-1818. Timbered areas dotted; prairie areas unmarked; no survey data were at hand for the extreme northeast corner of map or for St. Louis proper. Original Spanish grant outlined in heavy black; Wildwood proper is solid black. Square area lightly outlined and marked 12 is Section 12 in Township 46 North, Range 6 East. The town of Ferguson centers on the west boundary of Section 12. St. Ferdinand de Florissant is about 3 miles northwest of Wildwood. The prairie soil boundary is from Krusekopf, 1923.

Early Description

Figure 1 shows the original Spanish grant in heavy outline, and Wildwood (the wood-lot and residence area) in solid black. Maline Creek drains eastward through river-bottom woods into the Mississippi River, while to the west Coldwater Creek flows north into the Missouri. Wildwood is seen to lie between branches of Maline Creek, and consists of sloping land above cultivated bottoms to the east and south.

In 1817, shortly before the founding of the State of Missouri, extensive surveys were made of township and range lines in this area and details of topography and vegetation were recorded by the surveyors. From this material, preserved in the St. Louis County Engineer's office, it was possible to prepare fig. 1, which shows the distribution of forested and prairie land at that time. Hickories and Blackjack Oaks seemed to be the predominant types of trees. There is a strong tendency for the timber to be confined largely to the dissected headwaters of Maline Creek, and Gingras Creek and the River Des Peres to the south and west.

The surveyor, as he progressed along the range line of Section 12 a few chains east of Wildwood made the following remark: "Land rolling, soil rich and good for farming, thickly covered with oak and hickory". (Section 12 is indicated on fig. 1.) Significantly, however, he stated that halfway along this section line he built a mound (for a marker) in a "prairie," presumably a grass area surrounded by woods. Along the north boundary of the section the notation, "Prairie, good soil, scattering blackjacks and hickories," was made. On the west border the

country was "Gently rolling, scattering timber, blackjacks and oaks". It is thus vividly demonstrated that Wildwood was at the edge of the prairie. This fact plays a significant part in the history of Wildwood's vegetation.

On fig. 1 there also appears a soil boundary line. This was taken from the soil survey of the county made in 1923 (Krusekopf). It represents the easternmost limits (in the county) of the Tama silt loam, a rather well-developed prairie soil. To the east is what was then called the Memphis, a forest soil. Apparently those grasslands described by the old surveyors as being east and south of this soil boundary line had not been established for a long enough period to have their inevitable effect on the soil. The grass was invading land which inherently belonged to timber.

Fortunately, one of the early Government surveyors that worked in the region, a Mr. R. W. Wells, was interested in this prairie-forest problem. In his article (Wells, 1819) "On the origin of prairies," he made the following statement:

> ...the writer has seen, in the country between the Missouri and Mississippi, [precisely the area with which we are concerned] after unusually dry seasons, more than one hundred acres of woodland together converted [by fire] into prairie. And again, where the grass has been prevented from burning by accidental causes, or the prairie has been depastured by large herds of domestic cattle, it will assume, in a few years, the appearance of a young forest. Numerous proofs of this fact can be adduced but a few shall suffice. The vicinity of St. Louis and St. Charles affords instances. Both these beautiful places are situated on what are termed first and second bottoms, or flats—the former on the Mississippi, the latter on the Missouri; the second or upper bottoms, in both, are high plains that commence within a few hundred yards of the rivers, and extend back many miles; all the old French inhabitants will tell you, that the prairies formerly came immediately up to those places. Now the surrounding country for several miles is covered with a growth of trees of four or five inches diameter, near the towns where the burning first ceased, and gradually diminishing in size as you recede, until you at length gain the open prairies.

Nearly twenty years later another writer made observations which provide an interesting sequel to Mr. Wells' description. In his diary of a trip through the outskirts of St. Louis in 1836 Edmund Flagg has written:

> The face of the country is neither uniform nor broken, but undulates imperceptibly away, clothed in dense forests of blackjack oak, interspersed with thickets of the wild plum, the crabapple and the hazel. Thirty years ago the broad plain was a treeless, shrubless waste without a solitary farmhouse to break the monotony. But the annual fires were stopped, a young forest sprang into existence, delightful villas and country seats are now gleaming from the dark foliage in all directions.

It is difficult now for us to visualize our predecessors of 100 years ago living in a country of scrub oak, but such seems to have been the case. This change was not a uniform one, however. As Wells pointed out, it often began in the vicinity of settlements. It undoubtedly moved faster on some terraine than on others. That there was still considerable prairie left northwest of St. Louis at the time Flagg made his trip is shown by a letter which Evert A. Duyckinck wrote in 1837 in which he described a trip he made from St. Louis to Florissant:

> I must give you an early account of our yesterdays visit to the humorous little old town of Florissant situated in the midst of the flowers of the Prairie. . . . We were off before six o'clock. . . . We stopped on the rough edge of the Prairie which lies around the city where the scrub oak and marshy weeds ill set off by the thick fog gave us no im-

pression of the beautiful flowers and plants that lay beyond us in the fields to give so pretty a name to little Florissant. Here we breakfasted. . . . and were away again in the field. The mist gradually rolled away . . . & I had my first view of the Prairie rolling away & broken into innumerable landscapes with its unfenced fields of flowers and trees. A smooth level road lays through the Prairie which is rarely enclosed by fences and as B remarked it was a ride through a garden or the private lane on a gentleman's estate. (McDermott, 1944)

Wildwood Today

Wildwood was once one of those unfenced fields of trees. Today it still persists, though it is fenced and surrounded by suburbs instead of by prairie. It is mature now, even over-mature as the large number of dead and fallen trees on the diagramatic representation of the woods in fig. 2 show. Nearly one fifth of the trees had died in 1946. At the present writing the number has greatly increased. It is predominantly an oak-hickory woods. A complete tree-by-tree survey of the entire 41.5 acres in 1946 showed that Pignut Hickory, Black and Shingle oaks made up 54 per cent of the total. Twenty-one other species made up the rest of the population (Table I). A glance at fig. 2 suggests the open quality of the woods and shows the cow trails that have resulted from years of

TABLE I

ANALYSIS OF WILDWOOD BY TREE SPECIES (INCLUDING DEAD TREES)

Species	Dead	Alive	Total	% of Total	Frequency (% of zones in which found)
Black Walnut *(Juglans nigra)*		4	4	.5	13
Mockernut Hickory *(Carya tomentosa)*		2	2	.3	6
Pignut Hickory *(Carya ovalis)*	17	82	99	12.4	100
Shagbark Hickory *(Carya ovata)*		1	1	.1	6
White Oak *(Quercus alba)*	1	15	16	2.1	25
Post Oak *(Quercus stellata)*		3	3	.4	13
Red Oak *(Quercus rubra)*		4	4	.5	25
Black Oak *(Quercus velutina)*	*	101	101	12.6	81
Black Jack *(Quercus marilandica)*	1	29	30	3.8	56
Shingle Oak *(Quercus imbricaria)*	35	197	232	29.1	100
White Elm *(Ulmus americana)*		35	35	4.4	31
Slippery Elm *(Ulmus rubra)*	3	36	39	4.9	50
Hackberry *(Celtis occidentalis)*		11	11	1.4	13
Red Mulberry *(Morus rubra)*		2	2	.3	13
Sassafras *(Sassafras albidum)*		61	61	7.6	63
Sycamore *(Platanus occidentalis)*		2	2	.3	13
Black Cherry *(Prunus serotina)*	1	2	3	.4	13
Black Locust *(Robinia Pseudo-Acacia)*		2	2	.3	13
Ailanthus *(Ailanthus altissima)*		2	2	.3	6
Sugar Maple *(Acer saccharum)*	3	8	11	1.4	13
Silver Maple *(Acer saccharinum)*		2	2	.3	13
Box-Elder *(Acer Negundo)*		3	3	.4	13
Gray Dogwood *(Cornus racemosa)*		2	2	.3	13
Persimmon *(Diospyros virginiana)*	2	72	74	9.3	6
Oak, dead, species unidentified	30		30	3.8	63
Unidentified dead trees	26		26	3.3	63
Total	119	678	797		

* Included under dead oaks, below.

grazing. To locate particular areas and to get an idea as to which species were most widely distributed, the wood-lot was roughly divided into 16 zones by superimposing a grid. Table I shows the calculated frequency of the different species. Shingle Oak and Pignut Hickory occurred in all zones and Black Oak in all but three. Persimmon and Sassafras were the next most abundant trees though only the Sassafras was widely distributed, most of the persimmons being in a single copse.

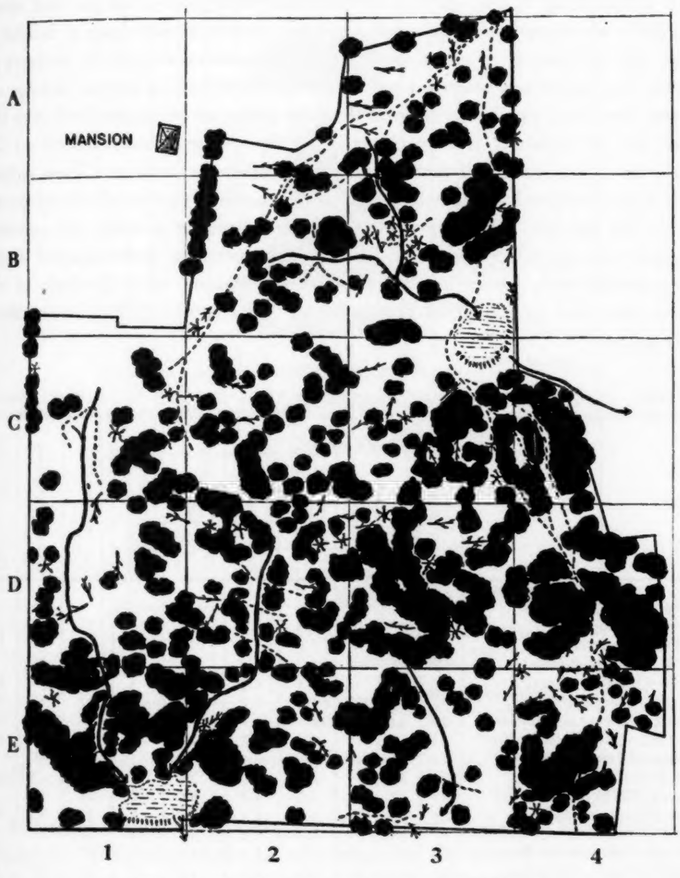

Fig. 2. Diagrammatic representation of Wildwood.

Solid black—Live trees
Radiating branches—Standing dead trees
Prone trunks—Fallen trees
Solid lines—Drainage
Dotted Lines—Cow paths
Hatchures—Dams
Horizontal and vertical lines divide Wildwood into zones

AGES AND THE PAST

In order to learn in more detail what Wildwood's role may have been in the transition from prairie to forest and to attempt to find out what influence successive phases of exploitation may have had, an intensive study was made of the ages of the trees in the woods. In some cases ages were obtained by simple stump counts, but ordinarily the procedure used was as follows: With an increment borer a core was procured from the desired tree, but since the borer available was only 10 inches long, it was only in smaller trees that ages could be read direct. Ordinarily it was necessary to procure cores and stump counts from a number of different sizes of trees of a given variety. Measurements of growth in years per inch were then made and averaged to reduce the error due to skewed boring, tree shape and diameter, and habit of growth. An index in years per inch was thus obtained for 16 different tree species (Table II). The circumferences of 222 trees selected at random in all parts of the woods were then taken. These circumferences were converted to diameters and ages, according to the calculated growth index for the species. These ages were then tabulated as averages of successive twenty-year periods taken every five years. These averages were adjusted so that they represented each species in proportion to the number of individuals of that species in the total woods population in 1946. The resulting graphs are shown in figs 3 and 4.

TABLE II

DIAMETERS, HEIGHTS, AND GROWTH RATES OF TREE SPECIES WITHIN WILDWOOD

Species	Ave. diam. breast high (inches)	Ave. height (feet)	H/D (feet)	Rate of growth in yrs. per in.		Ave. age allowing 1-inch bark for all species	Diam. smallest tree (inches)	Age smallest tree (years)	Diam. largest tree (inches)	Approx. age largest tree (years)
				Last inch	Entire tree excl. bark					
*BlackWalnut *(Juglans nigra)*	18	47	32				11		25	
Hickory *(Carya sp.)*	19	69	44	8.5	7.0	126	12	77	32	217
White Oak *(Quercus alba)*	27	82	37	3.3	4.2	109	9	34	37	151
*Post Oak *(Quercus stellata)*	15	53	43				11		27	
*Red Oak *(Quercus rubra)*				5.5	4.1				46	185
Black Oak *(Quercus velutina)*	31	83	32	6.6	4.8	144	18	82	46	216
Black Jack *(Quercus marilandica)*	26	56	26	8.5	5.6	140	16	84	44	240
Shingle Oak *(Quercus imbricaria)*	26	76	35	8.2	4.7	118	12	52	42	193
White Elm *(Ulmus americana)*	23	66	34	2.1	2.1	46	13	25	41	84
Slippery Elm *(Ulmus rubra)*	19	61	39	6.5	5.0	90	9	40	29	140
Hackberry *(Celtis occidentalis)*	15	42	34	5.5	3.8	53	10	34	19	68
Sassafras *(Sassafras albidum)*	24	48	24	6.	4.8	110	8	34	42	197
*Sycamore *(Platanus occidentalis)*	27	85	38	2.0	1.8	47	22	38	33	58
*Black Cherry *(Prunus serotina)*	22	71	39	10.5	5.4	114	14	69	29	151
*Ailanthus *(Ailanthus altissima)*	21	42	24	2.5	1.7	34	17	27	25	41
Sugar Maple *(Acer saccharum)*	14	48	41	7.3	5.5	72	9	44	29	154
*Silver Maple *(Acer saccharinum)*	25	87	42				19		31	
*Box-Elder *(Acer Negundo)*	21	55	31	7	5.6	112	17	90	24	129
Persimmon *(Diospyros virginiana)*	14	57	49	9.7	4.5	58	9	36	24	104
All Species	22	66	36	6.2	4.4	92	8		46	

* Numbers very limited

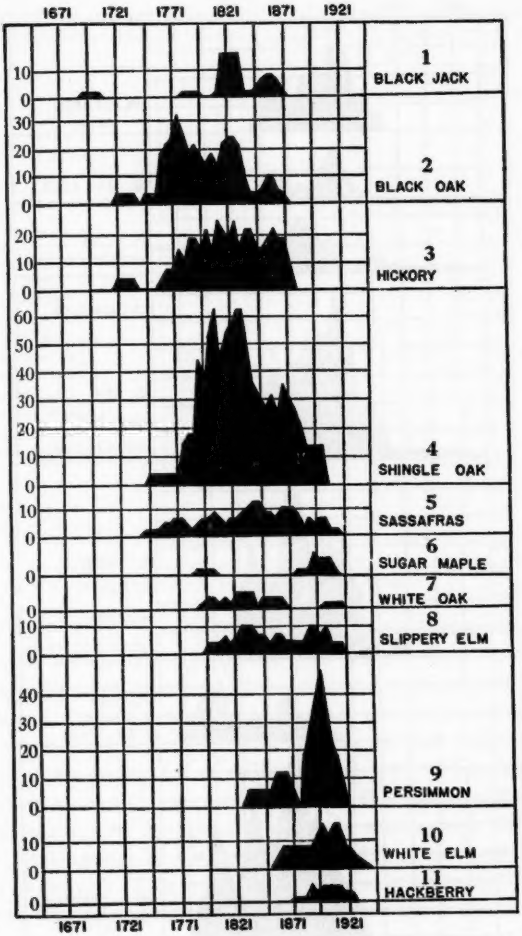

Fig. 3. Age distribution of various Wildwood tree species. Figures at left are numbers of individuals.

It seemed a reasonable possibility that graphs similar to those obtained from present-day Wildwood might be calculated for the witness trees used in old surveys, since diameters and species are given. Three surveys had been made in the area of the original Spanish grant, or on adjacent section lines at convenient times in the past: the original survey of 1818, and two subsequent ones in 1850 and 1871. They included a few areas as much as a half mile from Wildwood, but it is felt that conditions are sufficiently uniform for them to be useful. The numbers

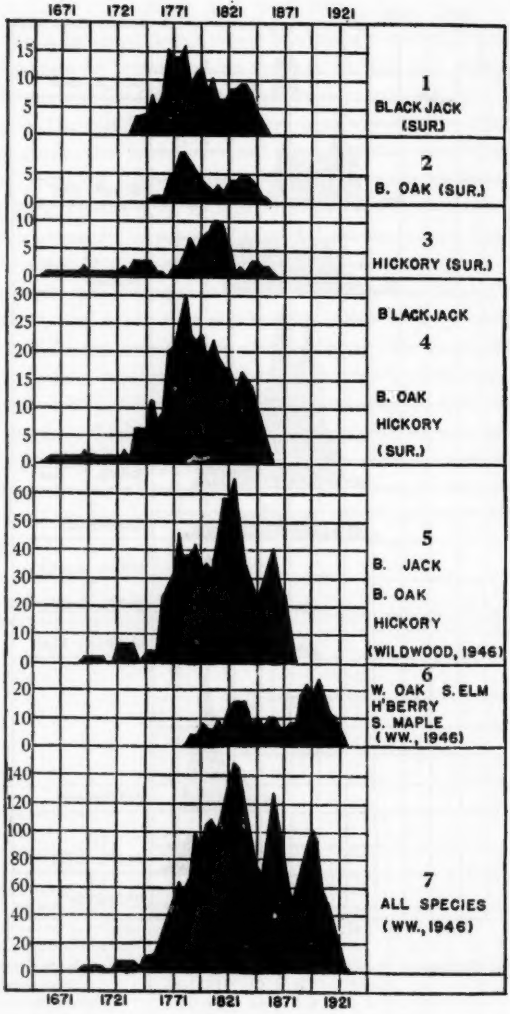

Fig. 4. Age distribution of trees of various species found in Wildwood, or listed as witness trees in surveys of 1821, 1850, and 1871. Figures at left are numbers of individuals.

and diameters of different species of witness trees are compared with the trees of the study area in Table III. By using the growth index for each species as calculated earlier, the ages of the survey trees were compiled, and all adjusted to date from 1946. A total of 99 trees was thus involved in the composite graph (fig. 4,

TABLE III

COMPARISON OF WITNESS TREE DATA WITH PRESENT DATA

Species	Year of survey											
	1818			1850			1871			1946*		
	Numb. of trees	% of total	Ave. diam. (inches)	Numb. of trees	% of total	Ave. diam. (inches)	Numb. of trees	% of total	Ave. diam. (inches)	Numb. of trees	% of total	Ave. diam. (inches)
Hickory *(Carya sp.)*	4	12	14	14	35.	12	11	23.	10	80	11.9	19
White Oak *(Quercus alba)*							2	4.	15	15	2.2	27
Post Oak *(Quercus stellata)*							1	2.	18	3	.4	15
Red Oak *(Quercus rubra)*	3	9	6				4	8.	15	4	.6	
Pin Oak *(Quercus palustris)*							6	13.	11			
Black Oak *(Quercus velutina)*	6	18	9	4	10.	5	11	23.	16	101	15.	31
Black Jack *(Quercus marilandica)*	20	61	9	21	53.	9	8	17.	13	27	4.	26
Sassafras *(Sassafras albidum)*							1	2.	7	53	7.9	24
Sycamore *(Platanus occidentalis)*				1	2.5	18				2	.3	28
Wild Cherry *(Prunus serotina)*							2	4.	12	2	.3	22
Cottonwood *(Populus deltoides)*							1	2.	18			
Total	33			40			47			287		
Number of species		4			4			10			24	
Ave. diam., all trees			10			9			12			24

* Only those trees are included in this column for which comparisons are available. All hickories are totalled together, since no differentiation was made in the survey.

No. 4) of the three species for which there were sufficient data. Separate graphs of the three species are given in fig. 4, Nos. 1, 2, and 3.

Considering the many possibilities of error in the application of such average growth indices and the heterogeneity of the data, the results are more than interesting. In fig. 4, No. 4 is the compilation of tree-age data from survey sources. Numbers 5 and 7 are summaries of Wildwood growth. These curves strongly suggest an abrupt increase in tree sprouting some time between 1745 and 1780. If only the last curve were available, it would be easy enough to attribute this rise merely to the longevity of the species involved, but the trees of the survey were measured as early as 1817, and at two subsequent intervals. Yet the curve begins to rise at the same place. Also, the fact that the curves are based on a composite of species is further evidence that it is not mere maturity which accounts for the sudden rise, for the maturity of species so diverse as hickory, Black Oak, and Blackjack would not be expected to coincide. The case is pretty strong for a rather abrupt increase in the sprouting of these species.

Previous to the 1745-1780 increase the data available strongly suggest a condition such as the surveyors describe as "scattered blackjacks and hickories." Where these early trees came from and whether they were invaders in an unstable prairie or remnants of an older forest, it is impossible to say. The broad open aspect of the oldest trees still alive and the reputation of blackjacks and hickories as invaders of cut-over and burned areas would suggest that they were the only

elements of the tree flora which were capable of maintaining themselves under prevailing conditions. Old climax growths of Sugar Maple, Basswood, Hackberry, or White Oak, if they ever existed, have been largely destroyed by fires, although a single Sugar Maple, completely hollow and fire scarred, must date back to 1800, and possibly even to 1750. This tree was on a moist northeast slope. In all probability islands of climax woods existed in moist protected areas, just as they seem to have done on some Wisconsin sites (Ellarson, 1949). Constant infection of prairies with seedlings and sprouts and constant scorching of wooded islands by fire were the order of the day. The balance was upset by forces operating in the last half of the eighteenth century. Is it mere coincidence that St. Louis was established in 1764, Florissant in 1785, Creve Coeur (a few miles west) in 1793? These early settlements were not made without disrupting the prevailing Indian population and consequently the firing practices described by Wells and Flagg. Even fires started by the white settlers or by natural causes would have been restricted by developing roads, crop land, timber clearing, the activities of domesticated animals, and hay cutting.

The composite curve of all species in Wildwood (fig. 4, No. 7) shows that the peak of tree invasion occurred about 1825, shortly after Missouri had become a state, and Mullanphy had taken over the property of Wildwood. This peak was largely the result of the intrusion of a large number of Shingle Oaks between 1800 and 1825. Apparently the grass had been sufficiently weakened and the proper amount of hazel and dogwood had grown up to permit the successful establishment of the Shingle Oak.

It is interesting that so-called virgin timber is a rare thing in much of the Middle West. Instead, there are remnants of these extensive oak forests which came in after the fires stopped. Such growths are seen in other states, especially Wisconsin and Iowa. In Wisconsin, however, the average age of these stands runs much closer to 105 or 110 years than 135. It is probably no coincidence that the rush of settlement to Wisconsin did not occur until about 1840 or so. In western Iowa even-aged stands of oaks which have come into the prairies are only some 80–90 years old. Western Iowa had a population of less than two people per square mile until 1855.

This relatively sudden disappearance of prairie land before the forests is sometimes attributed to climatic changes, but it is hardly likely that climatic change would have manifested itself so suddenly and so coincidentally with the white man's progress across the country. It is probable, however, that a climatic change of low intensity but of broad distribution had already occurred some time in the past, and had left the prairie-forest border in tension that could be easily upset by changed land use.

It is of some interest that by the time a peak of new forest growth had been reached, slightly more mesophytic types began to make noticeable progress through the woods. This is especially true of White Oaks and Slippery Elms (fig. 3, Nos. 7 and 8). Following the peak of 1825, new tree growth dropped to a low level

in 1850. We can only guess that this was associated with the heavy competition of the developing forest, or possibly it was related to some agricultural activity of a minor sort carried on by Mullanphy's tenants.

By 1865 a new surge of growth is evidenced in oak, hickory, persimmon, and sassafras. The Civil War was a period of considerable readjustment for society in general and particularly for that founded on slavery. We might surmise that Major LaMotte found it especially difficult to maintain his herds and other activities at Wildwood while the conflict was on, with the result that a new forest began to develop. Doubtless such an effect of the war would be evident over rather wide areas, and study on a more extensive scale might show it to have been general.

Following the war Major LaMotte's activity began in earnest. The decline of tree growth shown on the graph is undoubtedly associated with the increase of his herds. It may be significant also that by 1870 a railroad had been built just south of the woods, and fires probably caused some destruction to young trees. The tenant farmer, now nearly ninety and a resident of the area for some seventy years, recalled several serious fires started in this manner.

Major LaMotte died in 1892. By 1896 Wildwood had begun to be a tangle of new sprouts, this time of Persimmon, Sassafras, Hackberry, Sugar Maple, White Elm and Slippery Elm (fig. 4, No. 6). These trees were largely in the more moist parts of the woods, where seedlings could reproduce. Apparently conditions had progressed to the point where establishment of oak and hickory was not successful. In 1920, the advent of Mr. S——'s dairy changed the picture again. Cows and brush-cutting and burning put a complete stop to Wildwood's investment in future wood.

DENSITY OF WOODS

As another approach toward reconstruction of earlier conditions in Wildwood and vicinity, the density of the woods was considered. In 1946 there were 797 trees, dead and alive, on 41.5 acres—an average of 19 per acre. Although some trees have fallen and been chopped for kindling, split for fence-posts and burned to clear the pasture, it can well be seen that this woods was never at any time a fully-developed forest, or even-aged stand of hardwoods, for under such conditions Schnur (1937) indicates that in a stand averaging 100 years of age on an excellent site one might expect close to 150 trees per acre. This figure is obtained under ideal conditions of sprouting and unhampered growth. Wildwood has been pastured off and on for almost 100 years so that its normal cycle of reproduction could never have been achieved.

From a sample measurement of about one tenth of all the trees in the woods an average horizontal spread of 43 feet or about 1450 square feet was obtained. If the latter figure is multiplied by 797, a total acreage of 26.6 acres is shown to be directly beneath trees or occupied by fallen ones (the average fallen tree was found to cover an amount of ground practically equal to that of the living ones), leaving 14.9 acres of open pasture, which is fairly evenly distributed about the

woods (fig. 2). If all the 797 trees were evenly spaced within the area they would be about 55 feet apart. Of course, no such ideal spacing occurs. Along the east border the density is as high as 50 trees per acre while in the northwest portion the density drops to 11. The majority of the woods, however, has a density close to the average of 19.2 trees per acre.

It is interesting to compare this density to densities of the past woodland as indicated by data from the three early surveys already mentioned. Table IV shows the average distances and angles between witness trees from the surveyor's station. It was common practice to take trees as close to the section corner or survey marker as possible; in any case trees beyond 100 feet are not desirable. Within very broad limits, therefore, an average of the distances will be roughly indicative of the density of the woodland. In the same way an angle between two trees should be close to 90 degrees. The denser the woods the more choice the surveyor would have and a higher percentage of angles close to 90 degress would be expected. It is advisable also to take trees of fair size which are well established and give promise of long life. These data are not nearly as extensive as might be desirable, and it must be remembered that the conscientiousness of the surveyor and numerous other factors might affect the results. It is felt, however, that such figures, if properly pursued and compiled, could be used to indicate the condition of woodlands of the past over considerable areas.

The average tree of 1946 is much larger than that of any previous period. This is exaggerated by the present absence of small growth due to continual grazing. It is evident, however, that there are many trees in the woods which are larger than the largest tree during any other period. The average distance between trees, or from an arbitrary spot to the witness tree, compares closely in 1946,

TABLE IV

COMPARISONS INDICATIVE OF DENSITY OF WOODS IN VICINITY OF, OR IN, WILDWOOD DURING VARIOUS YEARS*

Year	Number of species	Number of trees	Diam. smallest tree (inches)	Diam. largest tree (inches)	Diam. average tree (inches)	Av. dist. of Witness tree (feet)	Angle between witness trees		
							% between 70° & 110°	% between 40° & 140°	% between 20° & 160°
1818	4	33	4	18	10	58	25	33	67
1850	4	40	2	28	9	74	21	63	68
1871	10	47	4	24	12	60	25	65	90
1946	24	287	8	46	24	55†			

* Data for 1818, 1850, and 1871 based on witness trees recorded in old property surveys.
† Average distance between trees if they were equally spaced over total area.

1871, and 1818. The survey in 1850 took smaller trees and larger trees than either of the other two surveys, had a smaller average tree size, and had a larger average distance between trees, suggesting that in the areas surveyed the trees were somewhat sparser. In the angles between witness trees there is no suggestion that the woodlands were sparser in 1850. In 1871 conditions would seem to have been closest to those of the present, with a greater variety of species, a larger average diameter, and a witness-tree distance similar to the distance between trees at present. The angle data also suggest a greater degree of selectivity than at any other period. One might expect the woods to be sparser now due to the death and disappearance of trees, and this might be true but for a brief intermission in grazing which permitted the sprouting of certain trees. Actually, however, there is little evidence that very many trees have died until just recently.

RATES OF GROWTH

The rates of growth (Table II) of the various tree species are all greater than are usual, showing that the soil and location are excellent. A White Oak 37 inches in diameter, from the average Missouri site, might be twice the age of the one in this woods which is 100 years old. The wide spacing of the trees in Wildwood would also encourage rapid growth. In most cases the last inch of growth has been very slow, especially in the Blackjacks, Shingle Oaks and Persimmons. This is probably due to a combination of factors, including the maturity of the trees, the competition of the grass sod, and perhaps even the establishment of a match factory nearby, from which strong fumes of sulphur commonly invade the woods.

The fastest-growing tree is *Ailanthus*, with an average of 1.7 years per inch. This is essentially a fence-line tree and is not an integral part of the wood-lot, though many show considerable promise of establishing themselves before long, for they are the only young trees which can withstand the nibbling of cows and horses. Sycamores with 1.8 and White Elms with 2.1 years per inch grow almost as fast. None of these trees predominates in the woods. The slowest growing tree is the hickory, with an average of 7 years per inch.

UNDER THE TREES

Upon entering the woods from the west one crosses a stile over a barbed wire fence. Through the overhanging branches of sassafras that line the fence one can see a broad pasture which in spring may be plain bright green, or dotted with yellow dandelions. In late summer it is clouded with the white bloom of boneset. In winter the scattered stems of weeds fall and the sod slowly loses its greenness.

Beyond this open pasture the trees begin: a hickory, a group of Shingle Oaks, irregular ranks of trees along the gullies extending toward the ridge. In the sun-filled patches between trees there are usually old stumps, or whole fallen trees which gather about them, in late summer, canopies of pokeberries. Great trees that die drop bark and twigs and change the sod beneath to a collection of weeds, including pennyroyal *(Hedeoma pulegioides)*, Three-seeded Mercury *(Acalypha vir-*

ginica) and Horse-Nettle *(Solanum carolinense)*. In the deep shade of Sugar Maples the ground remains bare except in spring when Aunt Lucy *(Elissia nyctelea)* and Spring Beauty *(Claytonia virginica)* take the brief opportunity to bloom and seed. In the low shade about the pond violets and smartweed *(Polygonum Hydropiper)* and Fog Fruit *(Lippia lanceolata)* almost exclude the bluegrass.

Most of the plants of the woods survive only because they are unpalatable to cows, or, like violets and buttercups, get a good start in spring before the pasturage is sufficient to permit grazing. Even though the cows are in the woods by April, plants with persistent underground rhizomes or bulbs such as May-apple *(Podophyllum peltatum)*, Green Dragon *(Arisaema Dracontium)*, *Viola* sp., Violet Wood-sorrel *(Oxalis violacea)*, and Yellow Star-Grass *(Hypoxis hirsuta)* flourish. Dwarf Larkspur *(Delphinium tricorne)*, Indian Tobacco *(Lobelia inflata)*, White Snakeroot *(Eupatorium rugosum)* and similar poisonous species appear here and there, but are avoided by the cows. In July, catnip *(Nepeta Cataria)*, Mountain Mint *(Pycnanthemum virginianum)* Hedge Mustard *(Sisymbrium officinale)*, smartweed *(Polygonum Hydropiper)*, and the nettles *(Urtica* sp.) appear in patches. Species that sprinkle the open pastures, such as milfoil *(Achillea Millefolium)*, Bull Thistle *(Cirsium vulgare)*, ironweed *(Vernonia* sp.), mullein *(Verbascum Thapsus)*, and fleabane *(Erigeron* sp.) bloom at various times during the season, but none rival the great surge of boneset *(Eupatorium serotinum)* in late summer.

There is little suggestion in the flora of any prairie influence and there are remarkable few true woodland plants (Appendix I). In a few relatively stable places beside fallen trees *Arisaema Dracontium* may appear, but no *A. triphyllum.* In the same place may be American Bell-flower *(Campanula americana)*. In a protected corner is a single clump of Sensitive Ferns *(Onoclea sensibilis)*. In the open pasture one may find in earliest spring bluets *(Houstonia minima)* and field pansies *(Viola Kitaibeliana)*. About the fences are patches of Spider Flowers *(Cleome spinosa)* and hemp *(Cannabis sativa)*. Thick clumps of Blue Mist flowers *(Eupatorium coelestinum)* and common balm *(Melissa officinalis)* are found in openings in the woods; in the wet places are Monkey Flowers *(Mimulus ringens)*, spearmint *(Mentha spicata)*, and the big Blue Lobelia *(Lobelia spicata)*.

Beneath these gaunt trees there is no distinguished company of plants. There are familiar weeds of both native and foreign origin, and some common wild flowers of intermediate habitats. Combined with Kentucky bluegrass they provide the typical understory for a pastured woods, or wooded pasture, whichever we may prefer to call Wildwood. While its flora is undistinguished, it is a complex dynamic environment. No balance exists as it does in open pasture or prairie or in a climax forest. Not only is there the subtle struggle between trees and grass, between weeds and grass, but there is the vigorous, daily-witnessed, positive destruction of plants and plant habitats by cows, by falling trees and branches, and by man's varied ingenuity. In many environments from day to day one can scarcely discern any changes beyond those inflicted by unusual weather conditions,

or the normal progression of the seasons. In Wildwood there is seldom a day that passes that there is not some visible alteration. One day the woods is burned, on another a fallen Shingle Oak is split for fence-posts, campfires are built, mushroom hunters collect a crop of fungi in the morning mist, squirrels are shot, cows push soil into the creek, the ponds dry up—everything is changing. It is an environment where weeds find many opportunities for establishment. The following list suggests some of them:

Livestock.—
- Patches of dung
- Hoofmarks in loose wet or thin sod
- Paths
- Closely grazed spots where grass is pulled up by roots
- Broken banks along streams

Man's activities.—
- Bare areas from which sod has been cut
- Disturbed soil where fence-posts are split
- Dumps of trash, ashes, and garbage
- Fence lines
- Tractor trails
- Campfire areas
- Burned litter and leaves
- Broken dams and drained ponds

Weed patches.—
- Weakened sod or bare soil next to rank weed growth

Fallen trees.—
- Rotten wood
- Sod killed by shade and changed soil composition
- Disturbed soil caused by fall of tree
- Upturned roots

Rainfall.—
- Deposits of eroded soil on grass
- Concentrations of litter caused by heavy rains
- Gullies washed free of leaves by heavy rains
- Bare areas of soil caused by standing water

Miscellaneous.—
- Ant hills
- Gopher hills
- Dung beetle diggings
- Dog scratchings at bases of trees
- Sour soil beside tree trunks

FLOWERING PERIODS

In an effort to arrive at some quantitative expression of the flora, phenological records were kept on the week of first bloom and peak of bloom of 70 species during the year 1946. The graphs of these data are shown in fig 5, Nos. 1 and 3, and are prepared by using the number of species beginning bloom or in peak of bloom during successive 24-day intervals. By way of comparison, curves translated from Anderson and Hubricht (1940) are given in fig. 5, Nos. 2 and 4. These are from composite data on several habitats in an area some 30 miles southwest of Wildwood. First-bloom data give a curve very similar in its major aspects to that for the peak-of-bloom, though the peaks are naturally earlier. Since first-bloom is less subject to personal judgment than peak-of-flowering it would seem that in many cases the former alone would suffice.

Graphs of flowering peaks of two habitats, woodland and meadow, copied from the above-cited work are here reproduced in fig. 5, Nos. 5 and 6. The graph for Wildwood bloom is seen to contain a suggestion of both these graphs with a somewhat subdued spring bloom and a strong late summer flowering. Undoubtedly many aspects of the history and environment of the flora are combined in these curves. One might consider such curves as floral spectra, capable of expressing

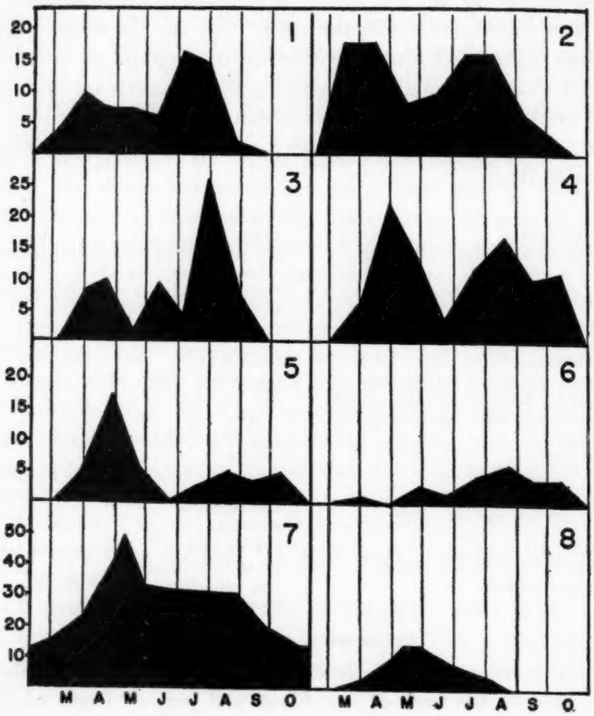

Fig. 5. Phenological graph of flowering, bird population, and nesting birds. Vertical figures, number of species; horizontal letters, months beginning with March.
No. 1—First bloom of 70 flower species in Wildwood.
No. 2—First bloom of 96 flower species compiled from data in Anderson and Hubricht (1940).
No. 3—Peak of bloom of 70 flower species in Wildwood.
No. 4—Peak of bloom of 96 flower species from graph in Anderson and Hubricht.
No. 5—Peak of bloom of woodland species from Anderson and Hubricht.
No. 6—Peak of bloom of 23 meadow species from Anderson and Hubricht.
No. 7—Number of species of birds in Wildwood during spring and summer, 1946. (Data for the fall migrations were not obtained. Winter population included 12 species.)
No. 8—Number of species nesting in Wildwood during summer, 1946.

the characteristics of an environment somewhat as absorption bands of the spectroscope express the chacteristics of a compound. Were enough accurate complete phenological data on restricted areas available, much valuable information concerning the organization of environments might become available, especially with reference to processes integrating plant and animal activities, and processes activating plant and animal growth and reproduction.

GROUND COVER

In the low southwest corner of Wildwood a survey of the plant population was made by estimating the proportion of ground covered by different species within the horizontal spread of sample trees. In Table V the results are tabulated by plant and tree species. The frequency and degree of dominance of each plant were calculated. Plant communities were nôt divided into different horizons, for tall weeds were not conspicuous. The figures are based on a hasty estimate of total plant coverage, not on basal area or number of individual plants. This was found to be a fairly satisfactory method for arriving at a rough mathematical conception of the vegetation. Bluegrass composed 29 per cent of the total. This is the only plant in the entire collection which provided any satisfactory stock food. Nimble Will *(Muhlenbergia Schreberi)* provided a random mouthful as did a few other grass species. The tips of smartweed were grazed carefully; tree seedlings and clover, though readily eaten, were very scarce. Plantain was eaten in early spring and blackberry leaves were eaten any time.

The sheer waste and inefficiency of pastured woods is made strikingly evident. Not more than 35 per cent of the entire vegetation in shaded areas is edible, and even that is of low feed value. No estimate of coverage was made in unshaded areas, but even assuming 90 per cent available pasturage (which is very generous) the total available pasturage throughout the 41.5 acres of Wildwood amounts to 22.7 acres or little more than one-half the total area. This leaves an average of one-half acre for each of the farmer's 43 head of stock during the grazing season. Little wonder he has to feed his cows heavily all year long. It is little wonder also that gullies and weeds grow faster than the grass, for hungry cows search the banks of creeks for grass and push the soil and sod into the path of washing water. They graze closely and walk unnecessary distances in search of food. The strain is more than thin sod can stand.

ANIMALS

Man's activities determine with the same consistency the nature of the animal community, for intensive grazing in a woodland discourages at least two-thirds of the normal population of wild life. The whole mid-section of the forest is removed and a void is left in which only occasional visitants play an active part. There are plenty of moles throughout the shaded part of the woods. In the full sun of the pasture along the fence-lines Pocket Gophers establish their mines. Short-tailed Shrews navigate beneath scattered leaves and logs. White-footed Mice keep their nocturnal appointments throughout the woods. Only two or three pairs of Cottontail Rabbits were seen within the limits of Wildwood, and these were near the fence lines. Chicken, Garter, and Black Snakes, toads, Box Turtles, and Painted Terrapins were sometimes seen, but none was common.

The lack of permanent cover is of the greatest importance in the life of these ground species. One might expect that the wealth of fallen trees would present an ideal arrangement for a variety of animals, but fallen trees disappear almost as if by magic beneath the devices of horns, hooves, and calloused tongues, aided by

TABLE V

ANALYSIS OF VEGETATION BENEATH 32 TREES
(AVERAGE HORIZONTAL SPREAD 43 FEET)

Species	Frequency of occurrence		Per cent of total area occupied
	Numb. trees under which found	Per cent	
Bromus secalinus	3	9	.4
Poa pratensis	30	94	29.2
Hordeum pusillum	1	3	
Agrostis perennans	5	16	2.4
Muhlenbergia Schreberi	27	88	16.6
Digitaria sanguinalis	4	13	.2
Setaria glauca	2	6	
Arisaema Dracontium	1	3	
Commelina communis	4	13	
Juncus tenuis	5	16	.4
Quercus (seedlings)	3	9	
Ulmus (seedlings)	14	44	.2
Morus rubra (seedlings)	6	19	
Urtica procera	2	6	1.0
Rumex Acetosella	5	16	.6
Polygonum Hydropiper	31	97	27.6
Chenopodium ambrosioides	3	9	
Phytolacca americana	19	59	4.1
Sassafras (sprouts)	2	6	
Lepidium virginicum	6	19	
Sisymbrium officinale	2	6	
Rubus sp.	3	9	
Trifolium repens	11	34	1.9
Oxalis europaea	6	19	.2
Acalypha ostryaefolia	5	16	.5
Rhus radicans	4	13	
Viola papilionacea	14	44	4.7
Sanicula canadensis	1	3	
Osmorhiza longistylis	1	3	
Diospyros virginiana	1	3	
Verbena urticifolia	9	28	.2
Lippia lanceolata	3	9	.1
Teucrium canadense	4	13	
Nepeta Cataria	1	3	
Glechoma hederacea	2	6	.4
Prunella vulgaris	2	6	
Hedeoma pulegioides	5	16	5
Melissa officinalis	1	3	
Mentha spicata	2	6	
Solanum carolinense	14	44	.5
Physalis pumila	3	9	
Verbascum Blattaria	1	3	
Verbascum Thapsus	1	3	
Scrophularia marilandica	4	13	
Plantago major	9	28	.5
Sambucus canadensis	10	31	
Lobelia inflata	1	3	
Vernonia altissima	2	6	
Eupatorium serotinum	31	97	6.2
Erigeron annuus	1	3	
Gnaphalium purpureum	3	9	.2
Ambrosia trifida	11	34	.4
Ambrosia artemisiifolia	2	6	
Cirsium vulgare	2	6	.2
Taraxacum officinale var. *palustre*	6	19	.4
Bare ground	4	13	1.2

molds and fungi. The average fallen tree is a coarse skeleton the first year. With the accumulation of leaves about the limbs fire destroys them rapidly. The trunk may linger much longer, harboring a succession of mold and insect life until the slow digestion of the log returns to the soil material borrowed a century before.

The empty lower elevations of the wood are seldom occupied unless it be by some brief gambol of a squirrel or by night a flying squirrel. Both Fox Squirrels and Gray Squirrels are found in quantity on the ground when nuts, acorns, or maple squirts are ripe. The rest of the time they are lost among the high branches or in hollow-tree dens. While surveying bird nests I had intended to estimate the number of den trees available in the woods, but the number of dens was soon found to exceed any possible demand. On the first of June and the next few days following, a total of 22 semi-permanent type leaf nests used for summer litters were counted, two of which were in old crows nests (fig. 6).

The squirrel-hunting season opened on May 30, and in the week following 41 squirrels were shot, and among those examined 18 were Fox and 16 were Gray Squirrels. The majority were young of the late winter breeding. After the first week very few squirrels were shot. The inexperienced young were decimated or educated and the older squirrels had retired to secret places for purposes closely related to the further propagation of the race. Many of the squirrels killed were on their way to and from mulberry trees. A majority were taken from the heights of oaks, in true Missouri style, with rifles, though shotguns and air-guns were also used. Since Wildwood is so surrounded by suburban developments the hunting pressure is extreme, and because of its small size and isolation it is not protected by wardens. The squirrels shot in the first week averaged one per acre. There could not have been less than two squirrels per acre at this time, and that is allowing a 50 per cent kill, which, though possible, probably is excessive even under great pressure. The ratio of Fox Squirrels to Gray Squirrels seemed to be about one to one. There was general agreement among the hunters that the Fox Squirrels were a relatively recent addition to the woods population. Two Black or Swamp Gray Squirrels were seen near a copse of persimmons, and a melanistic Fox Squirrel came regularly to the mulberry tree.

On moonlight nights a few perambulating opossums, in spite of their hoary camouflage, were easily discernible. Their droppings of persimmon seeds were occasionally found, suggesting how the isolated persimmon trees came to be scattered about the woods. No raccoons were discovered, although in the lower areas along Maline Creek their tracks were common. A Red Fox was occasionally seen, but he too came from the vicinity of the creek. The house cat was the dominant predator of the woods. Cats were the most frequent victims of a mammal trap I set for other animals. There were few days that one was not seen stalking grasshoppers, sparrows, or mice along the fence rows.

BIRDS

To the average person strolling through Wildwood the only wild life discernible consists of a few scattering birds. Few people would imagine that at least 84 different species could be seen within this small, seemingly uniform environment (Appendix II). In early May, a total of 49 different species were seen in a single morning. This is unusual, for the summer population would not consist of more than 31 species, of which only 21 actually nest in the woods. The number of species active during the months of February to October are graphed in fig. 5, No. 7. Nest activity is shown in fig. 5, No. 8.

In winter there are ordinarily 12 species of birds in the woods. Strangely, this number does not include the Chicadee and White-breasted Nuthatch. Something they need is missing. Nor does it now include the Great Horned Owl, which must have been there in the past. Only the Screech Owl remains to represent the Strigidae. Of the winter residents only a few are truly a part of the woods. The Sparrow Hawks are evident on any day as they ride the winter wind or balance on the spire of some dead tree. Bluejays are quiet, for once, and wait clumsily for spring. Crows crowd into the woods at evening or feed erratically there throughout the day, but more frequently seek the thicker woods in the valley. They are hunted vigorously by boys of the vicinity and during the previous year 96 were killed in the woods by one hunter. The titmouse is small but conspicuous by its voice. Woodpeckers, including the Downy, Hairy, and Red-bellied, and the Yellow-bellied Sapsucker, are evident in their undulating flight from tree to tree. These birds withstand the winter. There are no sparrows, for there is little cover from the searching hawks or from the wind. Cardinals appear occasionally enroute to more comfortable surroundings.

Spring is a different story. As early as late February and early March migrants begin to arrive. Loud thrasher songs begin in April and Bewick Wrens try out their collection of unfinished calls. May is the magic time. When the leaves come out the flame of Blackburnian Warblers and redstarts flash in the new green. Whole schools of warblers search restlessly, even in the rain. Then, as suddenly, the trees are empty, and occupied with the solemn business of secluding nesting birds.

It is interesting to compare the development of the bird-nesting season (fig. 5, No. 8) with flower bloom (fig. 5, No. 3). Both are influenced to a great extent by the leafing of trees, though in opposite ways, and while the peak of spring bloom is about the last week of April, just before the woods becomes shaded with new leaves, the nesting peak begins in the first week of May. Data on fall migrations were not obtained and consequently the curve in fig. 5, No. 7, is incomplete.

Figure 6 shows the distribution of 51 birds' nests which were discovered within the 41.5 acres of Wildwood. Of these, 5 were second nests of bluejays and 1 of a Bewick Wren. If we consider only first nestings there would be 45, or 1.1 nests per acre. This would mean a resident population of 90 birds or 2.2 mature birds per acre (ignoring the possibilities of polygamy). The total number of birds, assuming production of two young birds per nest (a generous estimate), would

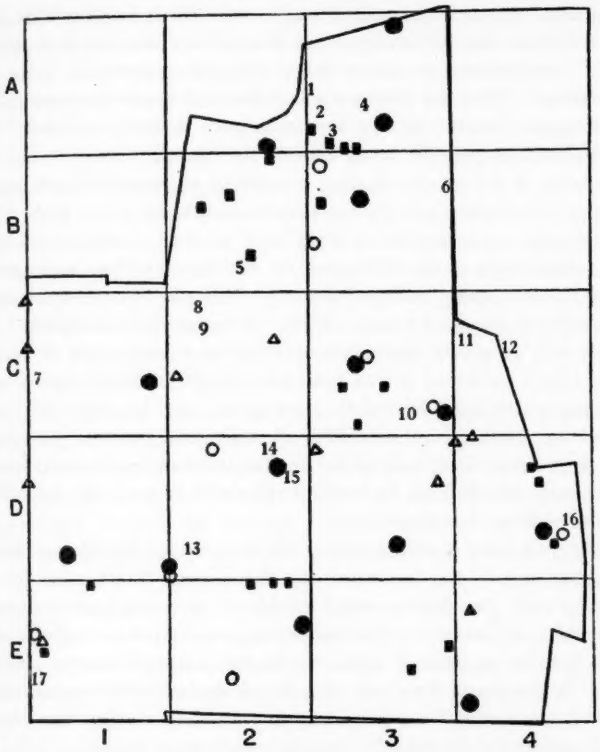

Fig. 6. Distribution of nests in Wildwood. Black dots—Red-headed Woodpecker; white circles—Flicker; black squares—Squirrel; triangle—Bluejay.

Number—as follows:

1. Bewick Wren
2. Bewick Wren
3. Crow
4. Hairy Woodpecker
5. Mourning Dove
6. Yellow-billed Cuckoo
7. Grackle
8. Titmouse
9. Robin
10. Red-bellied Woodpecker
11. Screech Owl
12. Thrasher
13. Crow
14. Wood Duck
15. Sparrowhawk
16. Sparrowhawk
17. Bluebird

have been, about the middle of June, 180 birds, or 4.3 birds per acre. Subsequent to this, second broods were raised in 10 Red-headed Woodpeckers' nests and in 1 Sparrow Hawk nest, and in the second nests of 5 bluejays and 1 Bewick Wren. If an average of two young birds per nest is assumed, 34 birds are added. This is a total of 214 birds.

Early in March the starlings began nesting and continued into August, though to a very much decreased extent. The first nesting was uniform and by far the

most important. It was begun early enough so that little conflict with other birds resulted. The fact that the starlings had chosen their nests made it easier on the Red-headed Woodpeckers to choose theirs when they arrived. There was very little quarreling. When the young starlings hatched there was some friction but nothing to suggest that the starling was causing the Redhead to suffer. The great number of nest holes probably eased some of the tension.

An estimate of the nesting starling population was made in early April. The later nestings were erratic and did not involve more than a few birds. The early nests were thickly concentrated, as many as 5 an acre. Those zones containing the highest percentages of dead Shingle Oaks and Slippery Elms were used. There were about 20 nests during the April nesting. This would mean 40 adults, assuming complete pairing, and 40 young. Added to the previous total of 214 this gives 294 birds in 41.5 acres or 7 birds per acre. The total production of young in the woods would have amounted to 186 from 130 old birds. These figures would not represent the population of the woods at any given time, but serve only to suggest their productivity in terms of bird life. Actually the pressure generated within the woods kept many birds busy along the borders and in adjacent fields. Starlings, once old enough to flock, gathered in the woods about cattle, or as frequently in the vicinity of the cow barns.

In the diagrammatic representation of the birds nests (fig. 6), one fact is most vividly demonstrated—the territorial distribution of Red-headed Woodpecker nests. Flicker nests also show a similar tendency, but being less numerous do not create as striking a pattern. After discovering the first 8 or 9 Redhead nests, I was able to predict where they should be found—simply a matter of waiting at a likely tree in the proper location. If no bird showed itself immediately, it was usually due to late mating; in a few weeks, by returning to the likely place, a nest was almost sure to be discovered. Fourteen nests were found of which 5 were predicted. Uniformity of habitat has much to do with the expression of territoriality. Where ideal conditions extend over sufficient area the manifestations of the behavior pattern have free rein to achieve an equilibrium.

Territories of the Redheads were defended carefully and consistently, but not with any great vengeance. A cautioning call, a flight in the general direction and the intruder left. Birds of other species were not objected to, as Redheads twice nested in the same trees with flickers and one Redhead built three feet from a Sparrow Hawk nest. When the young woodpeckers left the nest tree they gave evidence of a general conception of the adults' territory, but this may have been produced by their desire to remain near the parent bird for food, or by a natural disinclination to wander into unknown parts. During the second nesting of the Redheads defense of their territories became more of a problem, mostly as a result of intruding young of the first brood. These immature trespassers were promptly driven out. Special dispensations seem to have operated during mulberry and blackberry seasons so that traveling woodpeckers could pass through enemy territory unharmed, so long as they stayed on an established flight lane.

A Pileated Woodpecker was seen in late August, but none was seen to nest. There was ample evidence in the form of large squarish holes in many trunks that some time earlier this large woodpecker had been a common resident. The Wood Duck that nested in June was somewhat of a surprise, since it is commonly found nearer the Mississippi. Green Herons seemed strange visitors about the naked ponds, for there was no vegetation to conceal them, but a quick meal of tadpoles or small frogs was too much to resist.

Birds of more open country such as the Dickcissel, Meadowlark, Kingbird, Barn Swallow, and Indigo Bunting were only casual visitants and generally confined their activity to the fence-lines or the free air above the woods. None of these species nested in the woods, for the environment was not at all adaptable. Wildwood is essentially a woodpecker heaven, and of all the woodpeckers, the versatile Redhead seemed most comfortably settled and at home. His methods of feeding and nesting were admirably adapted.

It was no coincidence that the bird population included many species which fed by mounting low limbs, fence-posts, or stumps to watch for passing insects on the ground. Red-headed Woodpeckers, bluejays, bluebirds, Olive-backed and Hermit Thrushes, Sparrow Hawks and thrashers all participated regularly in this drop-to-the-ground method of feeding. Others such as cowbirds, starlings, grackles, and robins promenaded over the greensward itself, the first three species usually in the company of cows which uncovered and disturbed numerous insects and grubs which the patronizing blackbirds bowed to retrieve. Those birds which liked brush and bushes were frequenty visitors but rarely residents. Bewick Wrens took residence in two different fallen trunks and a thrasher nested in a growth of blackberries along the fence just out of the cows' reach. Most of these birds, however, such as the Catbird, Towhee, Swamp Sparrow, White-throated and Winter Wren were only present during migrations, or at times of bathing at the spring.

The analysis of the bird population of Wildwood is a subject that is inclined to lead one into a pleasant afternoon of thought, or an occasional morning of rare peace as the various species reveal their waking hours by their first song. A less aesthetic point of view might be desirable, but this study of Wildwood was never intended to be an altogether coldly analytical calculation of a beautiful place.

Conclusion

Wildwood is an isolated woodland which is slowly becoming more isolated. The slow progress of man across the fertile prairie and the rolling, thinly timbered land of St. Louis County which began in the eighteenth century has not stopped, and will not stop in the twentieth century. The resilient land, once soft with humus and rich with life, now produces sterile streets and careful rows of houses instead of wood or food. People call the soil "real-estate". Wildwood hangs on the verge of destruction. As a sanctuary of impressive beauty the woods can last only a little longer.

Wildwood was once a man's dream and then a man's possession. Major LaMotte, with pride and satisfaction, while on a trip east in 1875, wrote to his wife:

> We have seen so many sights, so much that is novel and interesting, that it appears a 'coons age' since we left Wildwood. But amid all this rambling 'thru pleasures and palaces', thru the charming and beautiful of this world's scenes, we invariably recur to the last word of the song, and apply them, with renewed warmth, to the land we left behind, that dear old Wildwood home.

Wildwood remains as a memorial to a man and a time. These ancient trees are strangely uneasy in 1953. They could crush a cluster of bungalows with the drop of a limb. They grew in the free earth, knowing only the lights of stars at night. They thrived on freedom, and the closing in of twentieth-century men upon them is a saddening, inevitable thing. It is the imminence of their destruction that has prompted me to know their story, to preserve them in words and figures, and in my understanding. They hold within them a part of the secret of life and of environments, part of the mystery of how this earth is organized. Their history is as important as mine.

Summary

A 40-acre woodlot 12 miles northwest of St. Louis was studied for a year from a broad ecological point of view with the object of recording its history, flora, and fauna before it is subdivided. The land was granted to a settler in 1799 by the Spanish governor. Through successive transfers the price rose from $1 an acre in 1804 to $30 in 1851, $300 in 1934, and $1000 in 1946. Exploitation of the land by the owner of a large estate began about 1850. Grazing has been permitted in the woods for nearly 100 years. Changes in the fortunes of the owners are reflected in the composition of the woodland.

Surveys made in 1817-18 described the land as being on the edge of the prairie, with scattered oak and hickory. Testimony of the surveyors concerned and contemporary travelers indicate the importance of fire in maintaining the grassland, and call attention to the influx of trees with settlement, these decreasing in size away from the towns. A soil survey of the area indicates the prairie of 1818 extended eastward over forest soil.

The entire tree population was plotted and found to average 19 trees per acre, with nearly one fifth of these recently dead. Over 54 per cent of the woods is made up of Shingle Oak, Black Oak and Pignut Hickory.

Ages of 222 trees in Wildwood were taken and the year of origin thus determined. These data suggest an increase in tree sprouting in the late eighteenth century, with an especially strong influx of Shingle Oaks between 1800 and 1830. Ages of witness trees from three early surveys substantiated this. Exploratory methods of using data from old surveys to determine density of woodlands are suggested. Rates of growth in the woods were very high, ranging from 1.7 to 7 years per inch. Sassafras, Shingle, Black, and Blackjack Oaks and one hickory over 200 years old were found.

The flora reflects the dynamic conditions that prevail in the woods, with cows,

fire, and fallen trees playing the major roles. Neither prairie nor woodland species are prominent. Curves of flowering peaks and flower initiation are presented and compared to those of other habitats. A hasty survey of plant cover under trees indicates less than 35 per cent edible forage in shaded areas. Grazing is at the rate of 2 head per acre from April to December, resulting in considerable erosion.

Bird and animal populations are described, and a survey of bird nests showed 71, with 11 second broods. The territorial distribution of Red-headed Woodpecker nests and flicker nests is described.

Epilogue

A few days after the manuscript for this paper had been sent in to the editor, circumstances permitted an early morning visit to Wildwood. My breath stopped when I came to the top of the hill where I had many times entered the woods. Instead of coming into the long shadows of its tall trees there was a gaping hole in the landscape. While the old mansion still remained secluded behind its curtain of Black Locust, the woods was gone—not a tree, not a plant, not a fence nor a cow. The long green sweep of pasture was a hill of yellow dirt yielding on every hand to bulldozers and scoops. The first row of skimpy houses was already up. On the wall of a shed was a plat of the development. I could not believe the ironic name it displayed. Forestwood! Not one of its future residents will be able to fathom why. The main street will be Meadowcrest—though asphalt and cement will cover the meadow.

Thus it is that we destroy the things we love the most! But I am thankful for one thing. The old farmer that had lived to 86 and for 50 years had milked Wildwood's cows by hand died only a few days before the first trees fell, and he will remember the woods as I have tried to describe it.

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Appendix I

PARTIAL LIST OF PLANT SPECIES FOUND IN WILDWOOD

(Arranged in natural order from Fernald, 1950)

Bromus secalinus L., Cheat
Poa annua L., Annual Bluegrass
Poa pratensis L., Kentucky Bluegrass
Dactylis glomerata L., Orchard Grass
Hordeum pusillum Nutt., Little Barley
Agrostis perennans (Walt.) Tuckerm., Upland Bent
Muhlenbergia Schreberi J. F. Gmel., Nimble Will
Eleusine indica (L.) Gaertn., Wiregrass
Digitaria sanguinalis (L.) Scop., Crab-Grass
Setaria glauca (L.) Beauv., Foxtail
Arisaema Dracontium (L.) Schott, Green Dragon
Commelina communis L., Creeping Dayflower
Juncus tenuis Willd.
Polygonatum canaliculatum (Muhl.) Pursh, Solomon's-Seal
Smilax herbacea L., Carrion-flower
Hypoxis hirsuta (L.) Coville, Stargrass
Sisyrinchium campestre Bicknell, Prairie Blue-eyed Grass
Salix nigra Marsh., Black Willow
Populus deltoides Marsh., Cottonwood
Juglans nigra L., Black Walnut
Carya ovata (Mill.) K. Koch, Shagbark Hickory
Carya tomentosa Nutt., Mockernut
Carya ovalis (Wang.) Sarg., Pignut Hickory
Quercus alba L., White Oak
Quercus stellata Wang., Post Oak
Quercus rubra L. var. *borealis* (Michx. f.) Farw., Northern Red Oak
Quercus velutina Lam., Black Oak
Quercus marilandica Muench., Black Jack
Quercus imbricaria Michx., Shingle Oak
Ulmus americana L., White Elm
Ulmus rubra Muhl., Slippery Elm
Celtis occidentalis L., Hackberry
Morus rubra L., Red Mulberry
Morus alba L., White Mulberry
Cannabis sativa L., Hemp
Urtica procera Muhl., Slender Nettle
Laportea canadensis (L.) Wedd., Wood-Nettle
Rumex crispus L., Yellow Dock
Rumex Acetosella L., Sheep Sorrel
Polygonum pensylvanicum L., Pinkweed
Polygonum Hydropiper L., Smartweed
Polygonum Persicaria L., Lady's Thumb
Chenopodium album (L.)., Lamb's Quarters
Chenopodium ambrosioides L., Mexican Tea
Phytolacca americana L., Pokeweed
Claytonia virginica L., Spring-beauty
Mollugo verticillata L., Carpetweed
Stellaria media (L.) Cyrillo, Common Chickweed
Stellaria pubera var. *silvatica* (Beguinot) Weath., Great Chickweed
Silene stellata (L.) Ait. f., Starry Campion
Ranunculus micranthus Nutt., Buttercup
Delphinium tricorne Michx., Dwarf Larkspur
Podophyllum peltatum L., May-apple
Sassafras albidum Nutt. var. *molle* (Raf.) Fern., Red Sassafras
Cleome spinosa Jacq., Spider-flower
Draba brachycarpa Nutt., Short-fruited Whitlow Grass
Thlaspi arvense L., Field Penny-Cress
Lepidium virginicum L., Peppergrass
Capsella Bursa-pastoris (L.) Medic., Shepherd's Purse
Sisymbrium officinale (L.) Scop., Hedge-Mustard
Platanus occidentalis L., Sycamore
Fragaria virginiana Duch. var. *illinoensis* (Prince) Gray, Wild Strawberry
Potentilla simplex Michx., Cinquefoil
Prunus serotina Ehrh., Black Cherry
Gleditsia triacanthos L., Honey-Locust
Trifolium repens L., White Clover
Robinia Pseudo-Acacia L., Black Locust
Oxalis violacea L., Violet Wood-Sorrel
Oxalis europaea Jord. f. *pilosella* Wieg., Yellow Wood-Sorrel
Geranium carolinianum L., Cranesbill
Ailanthus altissima (Mill.) Swingle, Tree of Heaven
Acalypha gracilens Gray, var. *monococca* Englm., Three-seeded Mercury
Acalypha ostryaefolia Riddell
Euphorbia maculata L., Eyebane
Callitriche deflexa A. Br., var. *Austini* (Englm.) Hegelm.
Rhus radicans L., Poison Ivy
Acer saccharum Marsh., Sugar Maple
Acer saccharinum L., Silver Maple
Acer Negundo L., Box-Elder
Parthenocissus quinquefolia (L.) Planch., Virginia Creeper

Vitis vulpina L., Frost or Chicken-Grape
Hypericum punctatum Lam., St. John's-Wort
Viola papilionacea Pursh, Meadow or Common Violet
Viola sororia Willd., Woolly Blue Violet
Viola pensylvanica Michx., Smooth Yellow Violet
Viola Kitaibeliana R. & S. var. *Rafinesquii* (Greene) Fern., Field Pansy
Sanicula canadensis L., Black Snakeroot
Osmorhiza longistylis (Torr.) DC., Smooth Sweet Cicely
Cornus racemosa Lam., Gray Dogwood
Diospyros virginiana L., Persimmon
Asclepias syriaca L. var. *kansana* (Vail) Palmer & Steyermark., Common Milkweed
Gonolobus Baldwinianus Sweet, Climbing Milkweed
Elissia Nyctelea L., Aunt Lucy
Verbena urticifolia L., White Vervain
Verbena stricta Vent., Hoary Vervain
Lippia lanceolata Michx. var. *recognita* Fern. & Grisc., Fog-fruit
Teucrium canadense L. var *virginicum* (L.) Eat., Wood-Sage
Nepeta Cataria L., Catnip
Glechoma hederacea L. var. *micrantha* Moricand, Ground-Ivy
Prunella vulgaris L., Heal-all
Lamium amplexicaule L., Henbit
Monarda fistulosa L., Wild Bergamot
Monarda citriodora Cerv., Lemon-Mint
Hedeoma pulegioides (L.) Pers., American Pennyroyal
Melissa officinalis L., Common Balm
Pycnanthemum virginianum (L.) Durand & Jackson, Mountain Mint
Mentha spicata L., Spearmint
Solanum nigrum L., Black Nightshade
Solanum carolinense L., Horse-Nettle
Physalis pumila Nutt., Ground-cherry
Datura Stramonium L. var. *Tatula* (L.) Torr., Purple Thorn-Apple
Verbascum Thapsus L., Common Mullein
Verbascum Blattaria L., Moth Mullein
Verbascum Blattaria f. *albiflorum* (Don) House
Scrophularia marilandica L., Figwort
Penstemon Digitalis Nutt., Beard-Tongue
Mimulus ringens L., Monkey Flower
Plantago major L., Plantain
Plantago Rugelii Dcne., Plantain
Plantago lanceolata L., Ribgrass
Galium Aparine L., Goosegrass
Houstonia minima Beck, Bluets
Sambucus canadensis L., Common Elderberry
Specularia perfoliata (L.) A. DC., Venus' Looking-Glass
Campanula americana L., Tall Bellflower
Lobelia siphilitica L., Blue Lobelia
Lobelia inflata L., Indian-tobacco
Vernonia altissima Nutt., Ironweed
Vernonia Baldwini Torr., Ironweed
Eupatorium serotinum Michx., Thoroughwort
Eupatorium rugosum Houtt., White Snakeroot
Eupatorium coelestinum L., Mistflower
Erigeron philadelphicus L., Fleabane
Erigeron annuus (L.) Pers., Daisy Fleabane
Erigeron strigosus Muhl., Daisy Fleabane
Erigeron canadensis L., Horse-weed
Gnaphalium purpureum L., Purple Cudweed
Ambrosia trifida L., Great Ragweed
Ambrosia artemisiifolia L. var. *elatior* (L.) Desc., Common Ragweed
Rudbeckia hirta L., Black-eyed Susan
Achillea Millefolium L., Common Yarrow
Chrysanthemum Leucanthemum L. var. *pinnatifidum* Lecoq & Lamotte, Ox-eye Daisy
Cirsium vulgare (Savi) Tenore, Common or Bull Thistle
Cichorium Intybus L., Chicory
Taraxacum officinale Weber var. *palustre* (Sm.) Blytt, Common dandelion
Lactuca scariola L., Prickly Lettuce

APPENDIX II

LIST OF BIRD SPECIES FOUND IN WILDWOOD

(Nomenclature from Bennitt, 1932)

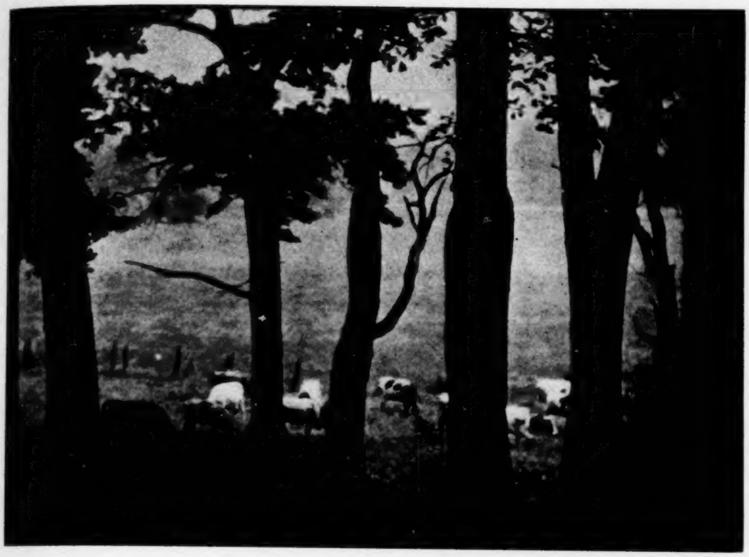
Great Blue Heron, *Ardea herodias herodias*
Eastern Green Heron, *Butorides virescens virescens*
Wood Duck, *Aix sponsa*
Sharp-shinned Hawk, *Accipiter velox velox*
Eastern Sparrow Hawk, *Falco sparverius sparverius*
Eastern Bob-white, *Colinus virginianus virginianus*
Killdeer, *Oxyechus vociferus vociferus*
Eastern Solitary Sandpiper, *Tringa solitaria solitaria*
Rock Dove, *Columbia livia livia*
Eastern Mourning Dove, *Zenaidura macroura carolinensis*
Yellow-billed Cuckoo, *Coccyzus americanus americanus*
Eastern Screech Owl, *Otus asio naevius*
Eastern Nighthawk, *Chordeiles minor minor*
Chimney-swift, *Chaetura pelagica*
Ruby-throated Hummingbird, *Archilochus colubris*
Eastern Belted Kingfisher, *Megaceryle alcyon alcyon*
Northern Flicker, *Colaptes auratus luteus*
Northern Pileated Woodpecker, *Ceophloeus pileatus abieticola*
Red-bellied Woodpecker, *Centurus carolinus*
Red-headed Woodpecker, *Melanerpes erythrocephalus*
Yellow-bellied Sapsucker, *Sphyrapicus varius varius*
Eastern Hairy Woodpecker, *Dryobates villosus villosus*
Northern Downy Woodpecker, *Dryobates pubescens medianus*
Eastern Kingbird, *Tyrannus tyrannus*
Northern Crested Flycatcher, *Myiarchus crinitus boreus*
Eastern Phoebe, *Sayornis phoebe*
Least Flycatcher, *Empidonax minimus*
Eastern Wood Pewee, *Myiochanes virens*
Barn Swallow, *Hirundo erythrogaster*
Purple Martin, *Progne subis subis*
Northern Bluejay, *Cyanocitta cristata cristata*
Eastern Crow, *Corvus brachyrhynchos brachyrhynchos*
Tufted Titmouse, *Baeolophus bicolor*
Red-breasted Nuthatch, *Sitta canadensis*
Brown Creeper, *Certhia familiaris americana*
Western House Wren, *Troglodytes aedon parkmani*
Eastern Winter Wren, *Nannus hiemalis hiemalis*
Bewick's Wren, *Thryomanes bewicki bewicki*
Eastern Mockingbird, *Mimus polyglottos polyglottos*
Catbird, *Dumetella carolinensis*
Brown Thrasher, *Toxostoma rufum*
Eastern Robin, *Turdus migratorius migratorius*
Wood Thrush, *Hylocichla mustelina*
Eastern Hermit Thrush, *Hylocichla guttata faxoni*
Eastern Olive-backed Thrush, *Hylocichla ustulata swainsoni*
Eastern Blue Bird, *Sialia sialis sialis*
Blue-grey Gnatcatcher, *Polioptila caerulea caerulea*
Eastern Golden-crowned Kinglet, *Regulus satrapa satrapa*
Eastern Ruby-crowned Kinglet, *Corthylio calendula calendula*
Cedar Waxwing, *Bombycilla cedrorum*
Starling, *Sturnus vulgaris vulgaris*
Yellow-throated Vireo, *Vireo flavifrons*
Blue-headed Vireo, *Vireo solitarius solitarius*
Red-eyed Vireo, *Vireo olivaceus*
Eastern Warbling Vireo, *Vireo gilvus gilvus*
Black-and-white Warbler, *Mniotilta varia*
Magnolia Warbler, *Dendroica magnolia*
Myrtle Warbler, *Dendroica coronata*
Black-throated Green Warbler, *Dendroica virens virens*
Blackburnian Warbler, *Dendroica fusca*
Chestnut-sided Warbler, *Dendroica pensylvanica*
Western Palm Warbler, *Dendroica palmarum palmarum*
Northern Yellow-throat, *Geothlypis trichas brachidactyla*
American Redstart, *Setophaga ruticilla*
English Sparrow, *Passer domesticus domesticus*
Eastern Meadowlark, *Sturnella magna magna*
Eastern Red-wing, *Agelaius phoeniceus phoeniceus*
Orchard Oriole, *Icterus spurius*
Baltimore Oriole, *Icterus galbula*

Bronzed Grackle, *Quiscalus quiscula aeneus*
Eastern Cowbird, *Molothrus ater ater*
Scarlet Tanager, *Piranga erythromelas*
Summer Tanager, *Piranga rubra rubra*
Eastern Cardinal, *Richmondena cardinalis cardinalis*
Rose-breasted Grosbeak, *Hedymeles ludovicianus*
Indigo Bunting, *Passerina cyanea*
Dickcissel, *Spiza americana*
Eastern Purple Finch, *Carpodacus purpureus purpureus*
Eastern Goldfinch, *Spinus tristis tristis*
Red-eyed Towhee, *Pipilo erythrophthalmus erythrophthalmus*
Slate-colored Junco, *Junco hyemalis hyemalis*
Eastern Chipping Sparrow, *Spizella passerina passerina*
White-throated Sparrow, *Zonotrichia albicollis*
Swamp Sparrow, *Melospiza georgiana*

Explanation of Plate

PLATE 27

Two views of Wildwood in 1952.



ETTER—WILDWOOD